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Fishery Bulletin

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NATIONAL MARINE FISHERIES SERVICE

Fishery Bulletin

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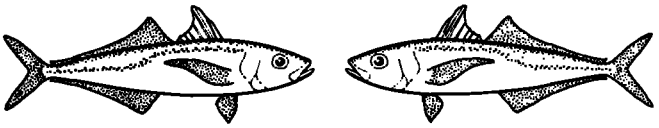
AWARDS



The Publications Advisory Committee of the National Marine Fisheries Service has announced the best publications authored by the NMFS scientists and published in the *Fishery Bulletin* for 1986 and the *Marine Fisheries Review* for 1985. Only effective and interpretive articles which significantly contribute to the understanding and knowledge of NMFS mission-related studies are eligible, and the following papers were judged as the best in meeting this requirement.

Fishery Bulletin 1986 — Starvation-induced mortality of young sea-caught jack mackerel, *Trachurus symmetricus*, determined with histological and morphological methods, by Gail M. Theilacker. Fish. Bull., U.S. 84: 1-17. Gail M. Theilacker is with the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA.

Marine Fisheries Review 1985 — Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California, by Susumu Kato and Stephen C. Schroeter. Mar. Fish. Rev. 47(3):1-20. Susumu Kato is with the Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA, and Stephen C. Schroeter is with the Department of Biological Sciences, University of California, University Park, CA.

INTERANNUAL VARIATION OF ICHTHYOPLANKTON COMPOSITION AND ABUNDANCE RELATIONS OFF NORTHERN CHILE, 1964–83

VALERIE J. LOEB[1] AND OMAR ROJAS[2]

ABSTRACT

Larval fishes were collected off of northern Chile during winter (July–September) ichthyoplankton surveys undertaken in 1964–70, 1972–73, and 1983. The 19-year timespan included a wide variety of hydrographic conditions in the Humboldt Current area (cold years, El Niño events, and intervening transition years); it also included the decline and collapse of the anchoveta fisheries and increases of sardine, mackerel, and jack mackerel stocks off northern Chile and Peru. The ichthyoplankton data are examined in relation to ambient hydrographic conditions as well as to possible chronological changes in environmental conditions which led to the increased Chilean sardine stocks and anchoveta fishery collapse.

More coherent patterns come from considerations of larval fish species composition in 1964–69 and 1970–73 data sets than from years of "similar" hydrographic conditions. A marked shift in relative abundances of nonfished mesopelagic species in 1969–70 is associated with changes within long-term physical data bases from Chile and Peru suggesting a large-scale environmental change. Sardine stock growth began with successful larval survival of 1968–69 and later year classes. Anchoveta stock decline began in 1972 probably due to poor larval survival. Affiliation of anchoveta and coastal species larval abundance implies that they are similarly influenced by coastal processes. An atmospherically driven oceanic circulation change beginning in the late 1960's and possibly involving onshore presence of subtropical and/or oceanic waters and altered coastal processes may have been responsible for the changes in the northern Chilean fish assemblages.

The Humboldt Current region, like the other major eastern boundary current systems (California, Benguela, and Canary Currents) is dominated by pelagic schooling fish stocks including anchoveta (*Engraulis*), sardine (*Sardinops*), hake (*Merluccius*), mackerel (*Scomber*), jack mackerel (*Trachurus*), and bonita (*Sarda*) (Parrish et al. 1983). These fish stocks, like those in the other eastern boundary current areas, exhibit extreme population fluctuations. Most notable in the past 30 years are the collapses of Peruvian and Chilean anchoveta stocks in the mid-1970's and their succession by sardine and, to a lesser extent, mackerel and jack mackerel stocks (Santander and Flores 1983; Serra 1983).

Hydrographic complexity and variability are characteristic of eastern boundary current systems. Included in the Humboldt Current region are equatorial, subequatorial, subantarctic, and antarctic oceanic water masses; northward flowing currents and opposing countercurrents; and wind driven, seasonally variable coastal upwelling (Wyrtki 1967). Additionally, the region is subject to 1) large seasonal and longer period fluctuations in advection of water masses of markedly different properties and 2) large interannual differences in the timing and intensity of seasonal upwelling processes (Bakun 1987; Bernal et al. 1983; Parrish et al. 1983; Robles et al. 1976). The clearest and generally considered most important of the nonseasonal processes influencing the biology of the current system is the El Niño phenomenon (Bernal et al. 1983; Guillén 1983). El Niño events off Peru and Chile are marked by large-scale atmospherically driven southward and coastward advection of warm, high-salinity equatorial and subequatorial surface waters, weakening of coastal upwelling (or upwelling of warm nutrient-poor waters), and weakening of subsequent phytoplankton blooms. These El Niño or warm-water periods are variable in their intensity and duration (Guillén 1983; Santander and Flores 1983). In contrast to these periods are more "normal" cold-water events resulting from atmospherically driven intensification of northward flowing cold, low-salinity subantarctic waters and seasonal upwelling of cold, nutrient-rich water. Major El Niño events occurred in 1891, 1925–26, 1940–41, 1957–58, 1965, 1972–73, 1976, and 1982–83;

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major cold events over the past 20 years occurred in 1964, 1967–68, 1970–71, and 1974–75 (Guillén 1983).

The decline and ultimate collapse of the anchoveta fisheries of Peru began in 1970 and was finalized by the intense 1972–73 El Niño; the northern Chilean stock decline started in 1972 and was finalized by 1977. Factors facilitating these declines are generally believed to include overfishing and the devastating effects of the El Niño on anchoveta spawning behavior and intensity as well as on subsequent recruitment. Competition and/or predation pressure resulting from increasing abundances and distributions of sardine and mackerel have also been hypothesized (Santander and Flores 1983; Serra 1983).

Because of the great socioeconomic value of the dominant pelagic fish species of the Peru-Chile ecosystem, their population fluctuations have received a great deal of attention over the past 20 years. However, coincidental changes in the composition, abundance, or spawning intensities of other commercially less important and nonharvested species have not been examined. Information on the changes of these unfished species in relation to hydrographic conditions and fluctuations of the dominant pelagic fish stocks provide additional insight into the ecology of the Humboldt Current and may elucidate possible causes for the dramatic changes which occurred during the 1970's.

In the present work we examine the abundance and composition of total ichthyoplankton assemblages collected off of northern Chile (lat. 18°-24°S) during 1964–73 and 1983 in relation to ambient hydrographic conditions. "Normal" cold water as well as warm-water and El Niño events occurred during the 19-yr sampling span. We also examine our results with respect to possible chronological change in environmental conditions which led to the 1977 anchoveta fishery collapse off northern Chile. Our results may be applicable for interpreting coincidental changes in the Peruvian ecosystem and may also be broadly applicable for studies of similar changes in the other eastern boundary current ecosystems.

METHODS

Samples were collected during 1964–73 and 1983 ichthyoplankton surveys conducted by the Instituto de Fomento Pesquero. The area most intensively surveyed was a narrow coastal strip extending between Arica and Antofagasta (lat. 18°-24°S, long. 70°-72°W; Fig. 1). This area includes one of two major anchoveta (*Engraulis ringens*) spawning grounds off Chile and the primary sardine (*Sardinops sagax*) spawning area off Chile prior to 1973 (Fig. 2A, B). All samples used for interannual comparisons were collected during late July–September following peak winter anchoveta and sardine spawning periods. Between 21 and 87 samples from the 18°–24°S area were analyzed for each of 11 cruises (Table 1). In one case data from two cruises (August and September 1968) were pooled to provide adequate coverage. Sampling was done annually from 1964 to 1970 and in 1972 and 1973. There was a 10-yr hiatus before regular sampling was resumed in 1983.

The 1964–73 samples were collected with Hensen nets (0.28 m^2 mouth opening; 300 μm mesh). Prior to 1973 the vertical net hauls were 50–0 m; in 1973 haul depth was increased to 100 m. The 1983 100–0 m vertical hauls were made with WP2 nets (0.25 m^2 mouth opening; UNESCO 1968) of 300 μm mesh. Samples were preserved using buffered 5% formalin solution. Sea surface temperature and salinity data were collected at most sampling stations for all but two winter cruises; these data are lacking for 1970 and salinity data are minimal for 1967.

All fish eggs and larvae were removed from samples, and invertebrate zooplankton biomass was measured. Wet weight displacement volume was measured for 1964–73 samples; in 1983 the Yashnov (1959) technique modified by Robertson (1970) was used. A calculated correction factor of 1.44 (±3.34) was applied to the 1983 biomass values to permit comparison with the earlier data.

All fish larvae were identified to lowest taxon possible and counted. We herein treat the larvae of six commercially important species (anchoveta [*Engraulis ringens*], Pacific sardine [*Sardinops sagax*], jack mackerel [*Trachurus murphyi*; also known as *T. symmetricus* in U.S.A.], chub mackerel [*Scomber japonicus*], South Pacific menhaden [*Ethmidium maculatum*], and hake [*Merluccius gayi*]) separately from the other 35 identified taxa. These six species are referred to as the "PL" (larvae of pelagic schooling species). The other larval taxa considered together are the "OL". The PL and OL categories are treated separately because abundances of the PL (especially of anchoveta and sardine) mask abundance rela-

FIGURE 1.—Ichthyoplankton study area between Arica and Antofagasta, Chile (18°–24°S), 1964–83.

tions of the OL. The OL are further separated into myctophid, "other mesopelagic" and "coastal" fractions.

Ichthyoplankton abundances are expressed as numbers per 10 m^2 sea surface. Flow meters were not used with the vertical Hensen net hauls; numbers of larvae caught in each tow are multiplied by 30 to provide numbers per 10 m^2 estimates. A flow meter used with WP2 nets provided water volume measurements and more accurate abundance estimates. Based on these measurements the conversion factor applied to Hensen net catches appears to be reasonable: water volumes filtered by 100–0 m vertical WP2 net hauls aver-

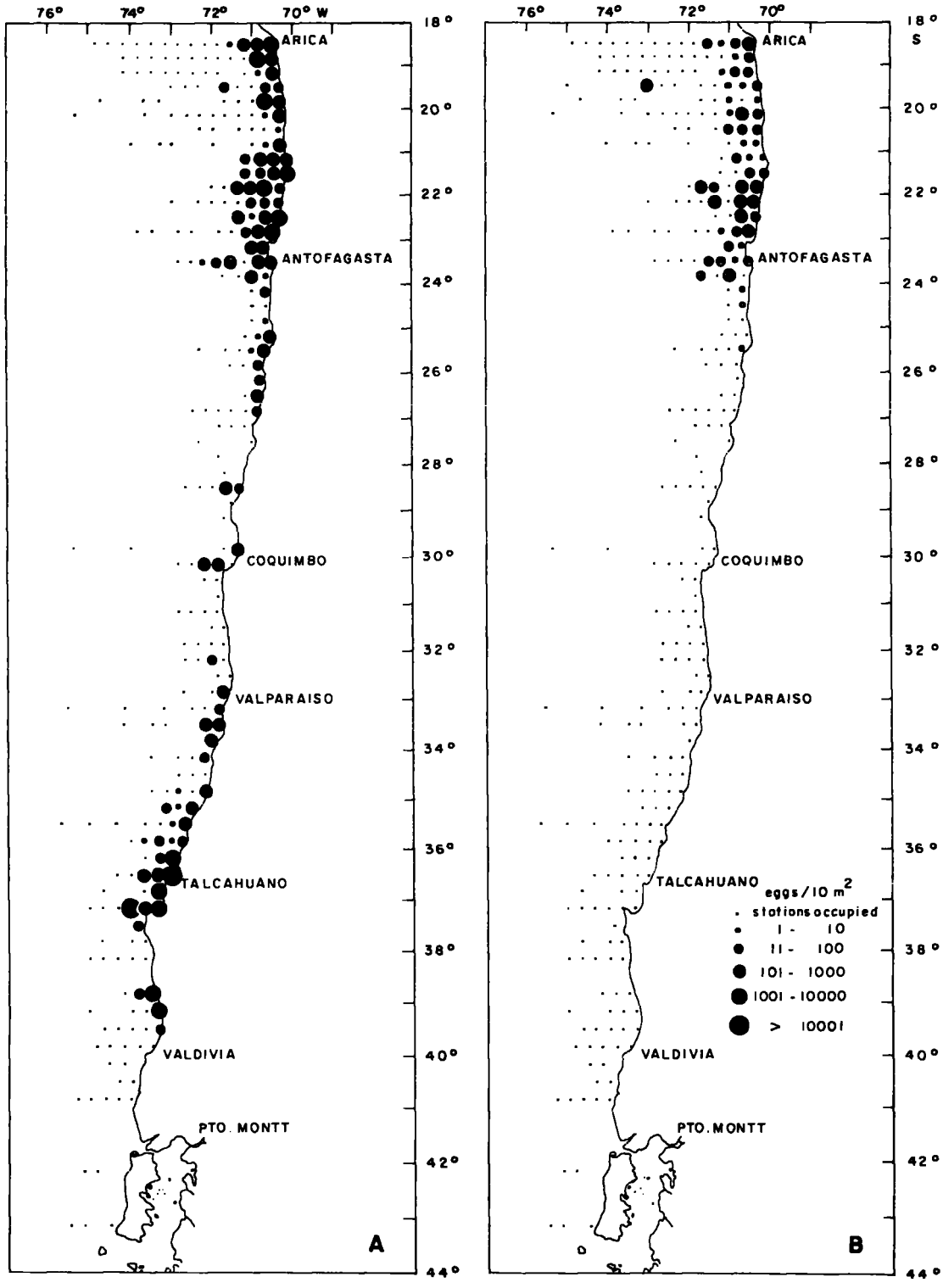

FIGURE 2.—Spawning areas of (A) anchoveta (*Engraulis ringens*) and (B) sardine (*Sardinops sagax*) off Chile based on egg abundances during July–September ichthyoplankton surveys, 1964–73.

TABLE 1.—Cruises yielding samples used for examination of ichthyoplankton abundance and composition variations off northern Chile. Only samples from 18°–24°S are used for interannual comparisons. Data from two 1968 cruises are combined; data from cruise 71(4)69CD are used for analysis of sampling depth-related catch differences. *N* = number of samples used in ichthyoplankton analyses. Tow types: H = Hensen net; WP2 = WP2 net; V = vertical.

Year	Cruise	Dates	Location		*N*	Tow	Type	Depth (m)
1964	06(3)64GE	16/08-23/09	18°20', 23°38'S	70°11', 71°50'W	68	H	V	0–50
1965	13(3)65CD	15/08-09/09	18°20', 23°50'S	70°00', 72°08'W	76	H	V	0–50
1966	25(3)66CD	21/08-31/09	18°28', 23°52'S	70°16', 72°16'W	72	H	V	0–50
1967	37(3)67CD	17/08-10/09	18°25', 23°45'S	70°05', 71°38'W	59	H	V	0–50
1968	47(3)68NO	25/08	18°28', 23°00'S	70°05', 70°58'W	37	H	V	0–50
	49(3)68NO	29/09	18°26', 23°01'S	70°11', 70°59'W	41	H	V	0–50
1969	70(3)69NO	23/08-25/08	18°29', 23°01'S	70°09', 71°10'W	35	H	V	0–50
	71(4)69CD	03/12-17/12	28°29', 38°00'S	71°22', 73°55'W	43	H	V	0–100
	71(4)69CD	03/12-17/12	28°29', 38°00'S	71°22', 73°55'W	39	H	V	0–50
1970	86(3)70NO	25/09-26/09	19°27', 21°58'S	70°14', 71°03'W	21	H	V	0–50
1972	109(3)72NO	04/09-15/09	18°29', 22°58'S	70°10', 71°25'W	87	H	V	0–50
1973	130(3)73CP	28/07-08/08	18°17', 23°08'S	70°05', 72°20'W	42	H	V	0–100
1983	277(3)83CP	07/08-15/09	18°33', 23°48'S	70°09', 71°38'W	38	WP2	V	0–100

aged 28.3 m^3 yielding a raw count to numbers per 10 m^2 conversion factor of 35; this 17% increase in conversion factor is associated with a 12% decrease in mouth opening of WP2 vs. Hensen nets. Larval fish diversity is expressed as total numbers of taxa per sampling period and mean numbers of taxa per tow.

Various parametric and nonparametric tests were used for statistical analyses. Differences in mean abundances are tested with 2-tailed *Z* tests and Mann Whitney U tests (Dixon and Massey 1969; Conover 1971). Similarity of abundance ranks within data sets are tested with Kendall's concordance (*W*) test (Tate and Clelland 1969) and Spearman's rho (ρ) correlation test (Conover 1971). Significant values resulting from these tests are indicated, but due to multiple testing these values should be used only as indicators of the relative strengths of relationships. Percent similarity indices (PSI; Whittaker 1975) are used for comparisons of species percentage composition. Because PSIs are strongly influenced by abundant species, we apply these tests to the OL fraction as well as to total larvae. We define as "high" all PSI values ≥80, as "moderate" PSI's ≥65 and <80, and as "low" values <65.

SAMPLING CONSIDERATIONS

Sampling Depth Differences

The 100 m sampling depths in 1973 and 1983 potentially effect direct comparisons of abundance estimates and species composition in these vs. earlier data sets owing to individual species' depth distributions. Evaluation of depth-related sampling differences is possible through a comparison of data obtained from coincidental 50–0 m and 100–0 m Hensen net samples taken during December 1969 at 28°–38°S (Table 1). These data indicate that abundance estimates and percentage contribution of the PL to total larvae were higher in 50 m tows while those of the OL were higher in 100 m tows (Table 2). Four of five PL species caught were more abundant and frequent in the 50 m samples. The greatest differences were for *Trachurus murphyi*, which was 5× more abundant and 3.6× more frequent, and *Merluccius gayi*, which was present only in 50 m samples. Abundance estimates were higher for 11 of 16 OL taxa in 100 m tows although, with a few exceptions, catch frequencies were similar. The greatest difference was for *Triphoturus mexi-*

TABLE 2.—Catch comparisons of 50–0 m and 100–0 m Hensen net tows taken at lat. 28°–38°S, long. 71°–74°W during 3–17 December 1969. Abundances expressed as mean and standard deviations of numbers per 10 m^2. F = percent frequency of occurrence in samples. Depth-related catch differences are shown as ratios of 50:100 m abundance estimates, species percentage contribution to total identified larvae, PL and OL percentage contribution to total larvae, and taxonomic diversity (mean numbers per tow and total numbers of taxa). *N* = number of samples. PL = larvae of pelagic species; OL = other larval taxa.

	50–0 m (*N* = 43)				100–0 m (*N* = 39)				
Taxon	$\bar{X}$	(S)	F	%	$\bar{X}$	(S)	F	%	Ratio
Engraulis ringens	34.2	(122.8)	23.2	13.42	22.3	(69.4)	15.4	7.23	1.53
Clupea bentincki	6.3	(28.2)	9.3	2.47	1.5	(6.7)	5.1	0.49	4.20
Ethmidium maculatum	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Merluccius gayi	1.4	(6.4)	4.6	0.55					
Trachurus murphyi	4.2	(14.0)	9.3	1.65	0.8	(4.8)	2.6	0.26	5.25
Total PL	46.8	(131.1)	34.9	18.36	25.4	(71.0)	23.1	8.24	1.84
Bathylagus nigrigenys	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Vinciguerria lucetia	10.5	(33.9)	14.0	4.12	16.9	(75.6)	7.7	5.48	0.62
Diogenichthys spp.	31.4	(107.0)	20.9	12.32	37.7	(79.9)	28.2	12.22	0.83
Hygophum bruuni	121.4	(238.2)	58.1	47.64	166.2	(291.0)	53.8	53.86	0.73
Protomyctophum sp.					3.1	(9.2)	10.3	1.00	
Diaphus sp.	7.7	(18.6)	18.6	3.02	9.2	(24.0)	17.9	2.98	0.84
Lampanyctus parvicauda	7.7	(18.6)	16.3	3.02	6.9	(21.2)	15.4	2.24	1.12
Lampanyctus sp.	1.4	(6.4)	4.6	0.55	1.5	(6.7)	5.1	0.49	0.93
Triphoturus mexicanus	7.7	(21.8)	14.0	3.02	18.5	(57.4)	20.5	5.99	0.42
Scopelosaurus sp.					0.8	(4.8)	2.6	0.26	
Normanichthys crockeri	15.3	(38.9)	18.6	6.00	20.0	(66.5)	10.3	6.48	0.76
Sebastes sp.	1.4	(9.1)	2.3	0.55	0.8	(4.8)	2.6	0.26	1.75
Blenniid A	0.7	(4.6)	2.3	0.27					
Blenniid D	0.7	(4.6)	2.3	0.27	0.8	(4.8)	2.6	0.26	0.88
Bothid	0.7	(4.6)	2.3	0.27					
Unid. 2	0.7	(4.6)	2.3	0.27					
Small damaged myctophids	4.8				9.2				
Other unidentified	13.2				7.0				
Total OL	226.0	(316.0)	86.0	81.59	299.4	(405.9)	82.0	91.78	0.84
Total larvae	272.8	(340.7)			324.8	(400.0)			0.84
No. taxa/tow	2.5	(2.0)			2.2	(2.0)			1.13
Total no. taxa	18				17				0.94

canus which was 2.4× more abundant and 1.5× more frequent in 100 m tows. Because of the large catch variability, none of the species abundance differences nor the abundance differences of the PL, OL, and total larvae are significant (*Z* tests, *P*'s all >0.10). Additionally, species abundances within all positive tows from the two sampling depths are not significantly different (Mann Whitney U tests, $P > 0.10$ in all cases).

The overall species composition of 50 and 100 m tows was similar. Despite greater proportions of PL in 50 m tows, the PSI value from comparisons of total species lists was high (87.7). Species percentage contribution within the OL fraction of the two tow types was also quite similar (94.5). Species abundance rankings within the two total larval data sets are significantly correlated ($\rho = +0.80$; $P < 0.01$). Species diversity estimates (total numbers of taxa and mean numbers of taxa per tow) are also similar.

From these comparisons it is apparent that the PL predominantly occur within the upper 50 m. Similar shallow (e.g., ≤50 m) distributions have been described for dominant PL species off of Peru (anchoveta, sardine, and hake; Sameoto 1982). The generally lower 100 m abundance estimates of these species is puzzling, but suggests possibly shorter sampling time and/or less efficient sampling within the upper 50 m of these tows. Higher catch frequency and abundance of *T. mexicanus* in 100 m tows suggest that large proportions (e.g., 30–60%) of these larvae are at 50–100 m.

As a result of these catch differences we suggest caution in making direct numerical comparisons between the 1973 and 1983 vs. earlier data sets. Although the overall compositions and abundance relations should not be markedly altered, some accommodation should be allowed for the percentage contributions and across-year abundance ranks of PL species (especially *Trachurus*) and *Triphoturus mexicanus*.

Net Type Differences

There are no data available for a direct evaluation of catch differences between the vertical Hensen and WP2 net tows. However, comparisons of data from the 1983 WP2 net hauls (Table 3) do not indicate that this net is more or less efficient than the Hensen net. Mean abundances and species diversity (total numbers of taxa and mean numbers of taxa per tow) are within the ranges of values from Hensen net tows.

Day-Night Catch Considerations

Day and night sample data have been combined for each cruise. Day samples (0600–1800 hours) outnumbered (generally 55–64%) night samples during all cruises. In nine cases there were non-significant day-night larval catch differences (Z tests, $P > 0.05$) and overall similarity in night: day catch ratios (0.74–1.8:1; mode = 1.2:1). One cruise had a significantly higher night vs. day catch (2.5×; $P < 0.01$); this cruise and one with

TABLE 3.—Abundance estimates and diversity of larval fishes and abundance estimates of zooplankton collected in July-September samples off northern Chile (18°–24°S), 1964–83. Larval fish abundances as mean numbers per 10 m². PL = larvae of commercially important pelagic species; OL = other larval taxa (myctophid, other mesopelagic, and other categories). Number of larvae is total raw count of identified larvae for each sampling period. Larval fish diversity expressed as total number of identified taxa and mean number of taxa per tow. Zooplankton abundance is mean displacement volume (cc/10 m²). N.A. = data not available.

	Mean abundance for									
Taxon	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Engraulis ringens	302.0	36.7	3,478.3	224.7	72.3	181.7	620.0	1,634.1	1,816.4	—
Sardinops sagax	5.3	5.1	12.5	4.6	21.1	24.9	1.4	327.2	52.1	594.9
Ethmidium maculatum	—	—	—	—	—	2.6	—	0.7	—	—
Trachurus murphyi	2.6	7.1	10.8	3.1	0.4	6.8	5.7	100.3	2.1	—
Scomber japonicus	—	0.4	—	—	—	—	—	25.9	—	—
Merluccius gayi	—	—	—	—	—	—	—	—	0.7	2.6
Total PL	309.9	49.3	3,501.6	232.4	93.8	216.0	627.1	2,088.2	1,871.3	597.5
Bathylagus nigrigenys	4.0	5.1	6.7	9.7	6.2	0.9	7.2	56.6	35.0	31.5
Vinciguerria lucetia	3.1	0.4	2.9	6.1	3.1	2.6	21.4	54.8	18.6	3.7
Sternoptyx diaphana	—	—	—	—	—	—	—	0.7	0.7	1.0
Chauliodus sp.	—	—	—	—	—	—	—	0.3	—	—
Stomias spp.	—	—	—	—	—	—	—	—	—	1.9
Lestidiops pacificum	—	—	—	—	—	—	—	0.3	0.7	—
Melamphaes sp.	—	—	—	0.5	0.4	—	—	0.3	2.1	—
Beryciform	—	—	—	—	—	—	1.4	—	—	—
Other mesopelagics	7.1	5.5	9.6	16.3	9.7	3.5	30.0	113.0	57.1	38.1
Diogenichthys spp.	6.2	18.9	14.6	30.5	7.3	14.6	21.4	59.3	39.3	114.2
Hygophum bruuni	—	2.8	1.2	3.6	—	—	—	—	—	0.9
Hygophum atratum	—	—	—	—	—	—	—	—	—	6.7
Metelectrona ventralis	—	—	—	—	—	—	—	—	—	0.9
Myctophum nitidulum	0.4	—	0.4	—	0.4	0.9	—	4.8	4.3	4.6
Diaphus sp.	—	0.4	0.4	—	—	—	1.4	0.3	—	4.5
Lampanyctus parvicauda	41.0	32.0	65.8	63.0	10.8	38.6	5.7	29.7	12.1	15.5
Lampanyctus spp.	—	—	0.8	—	1.1	—	—	—	0.7	—
Triphoturus mexicanus	31.8	15.8	20.8	29.0	4.6	31.7	11.4	19.7	23.6	33.6
Myctophids	79.4	69.9	104.0	126.1	24.2	85.8	39.9	113.8	80.0	180.9
Normanichtys crockeri	17.2	1.5	281.2	5.6	2.3	26.6	10.0	2.4	31.4	—
Sebastes sp.	0.4	—	2.5	1.0	0.8	—	—	—	0.7	—
Gadiform D	—	—	0.8	—	—	—	—	—	—	—
Macrourid A	—	—	—	0.5	—	—	—	—	0.7	—
Macrourid C	—	—	—	0.5	—	—	—	—	—	—
Blenniid A	0.4	—	0.8	—	1.2	—	—	—	1.4	—
Blenniid B	—	—	0.4	—	—	—	—	—	—	—
Blenniid C	—	—	—	1.5	—	—	—	0.3	—	—
Blenniid D	5.3	0.4	16.7	7.1	4.2	2.6	—	2.8	8.6	1.0
Gobiesocid A	0.4	—	0.8	—	—	—	—	1.0	0.7	—
Gobiesocid B	—	—	—	—	0.4	—	—	—	—	—
Unid. 1	—	—	—	—	0.8	—	—	—	5.7	8.6
Unid. 2	—	—	0.4	—	—	—	—	0.3	12.1	—
Unid. 3	—	—	—	—	0.4	1.7	—	0.3	0.7	—
Unid. 4	—	—	—	—	—	—	—	0.3	0.7	—
Ophidiid	—	—	—	1.0	0.8	—	—	—	—	—
Hippoglossina sp.	—	—	—	—	—	—	—	0.3	—	—
Other larvae	23.7	1.9	303.6	17.2	10.9	30.9	10.0	7.7	62.7	9.6
Total OL	110.2	77.3	417.2	159.6	44.8	120.2	79.9	234.5	199.8	228.4

TABLE 3.—*Continued*.

Taxon	Mean abundance for 1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Larval fish abundance and diversity										
Total ID PL	309.9	49.3	3,501.6	232.4	93.8	216.0	627.1	2,088.2	1,871.3	597.5
Total ID OL	110.2	77.3	417.2	159.6	44.8	120.2	79.9	234.5	199.8	228.6
Total ID larvae	420.1	126.6	3,918.8	392.0	138.6	336.2	707.0	2,322.7	2,071.1	826.1
Unid/missing OL	10.2	4.4	17.0	22.0	3.4	11.9	7.2	104.5	57.2	76.6
Total larvae	430.3	131.0	3,935.8	414.0	142.0	348.1	714.2	2,427.2	2,128.3	902.7
Number of larvae	953	321	9,406	771	360	650	495	6,738	2,900	893
Number of taxa	15	14	20	19	20	13	12	26	25	19
Number of taxa/tow	2.2	1.6	3.2	2.5	1.4	1.9	2.3	5.3	4.1	3.7
Number of samples	68	76	72	59	78	35	21	87	42	38
Zooplankton abundance	333.9	242.2	406.5	370.8	279.2	141.0	N.A.	301.7	100.6	168.7
Number of samples	85	124	72	59	78	35		110	42	30

a 1.8:1 night:day catch ratio were represented by fairly equal day (55–57%) and night samples.

TAXONOMIC PROBLEMS

The 576 samples used for interannual comparisons yielded a total of 41 taxa including 19 species, 7 genera, and 11 higher taxa (Table 4). The PL and most mesopelagic forms were identified to species. During several cruises there were large proportions of small *Diogenichthys* spp. (Myctophidae) larvae which could not be identified to species. As a consequence, data on the two species, *D. atlanticus* and *D. laternatus*, were lumped to permit reasonable between-year taxonomic composition comparisons. In all but one cruise, *D. laternatus* dominated (77–100%) the identifiable *Diogenichthys* larvae. Total within-year *Diogenichthys* spp. abundances were multiplied by proportions of identified *D. laternatus* and *D. atlanticus* larvae to provide between-year abundance rankings for each species.

Species identifications of coastal forms are limited by inadequate taxonomic information and by the presence of generally early larval developmental stages in samples. These larvae are primarily classified at familial and ordinal levels. Because the classifications include few multispecies groupings and those were numerically rare the taxonomic limitations offer no severe analytical problems.

Largest taxonomic problems occurred in cruises when large numbers of small unidentifiable larvae were caught (e.g., 1972 and 1983; Table 3). Additionally, most cruises had "missing" larvae (e.g., "other larvae" enumerated when the samples were first processed but not accounted for during later species identification work). With the exception of 1983 the unidentified and missing larvae made up ≤5% of the total larval abundance for each sampling period.

RESULTS

Overall Ichthyoplankton Composition

The 576 July–September samples used for interannual comparisons yielded a total of 23,487 identified larvae. These larvae were dominated (85.1%) by PL species (Table 4). Overall dominants were anchoveta (*Engraulis ringens;* 74.3%) and sardine (*Sardinops sagax*; 9.3%). The other PL species were relatively rare: *Trachurus murphyi* contributed 1.2% and *Scomber japonicus, Merluccius gayi*, and *Ethmidium maculatum* together formed 0.3% of the total. The larval abundances of these species off of Chile are strongly influenced by sampling time and location. *Merluccius gayi* occurs primarily to the south of the study area (24°–43°S) and *Scomber japonicus* and *Trachurus murphyi* have later summer (November–February) spawning peaks.

The OL were dominated by mesopelagic fishes (18 taxa, 10.6% of total larvae). Myctophids were most abundant (8.0%) primarily because of the large numbers of *Diogenichthys* spp., *Lampanyctus parvicauda*, and *Triphoturus mexicanus*, which together made up 7.7% of the total. One bathylagid (*Bathylagus nigrigenys*) and one gonostomatid (*Vinciguerria lucetia*) were also relatively abundant (together 2.5%). Coastal fish larvae (14 taxa) made up 4.2% of the total; a scorpaeniform (*Normanichthys crockeri*; 3.4%) and blenniid (Blenniid D; 0.4%) dominated this group.

Eighteen taxa were relatively frequent (e.g., in

≥50% of cruises) and/or abundant across the 10 sampling periods (Table 4). These taxa (four PL species, seven myctophid taxa, two other mesopelagic species, and five coastal forms) made up 99.6% of the identified larvae; they also contributed 97–100% of the identified larvae (91.2–99.6% of total larvae) and included the top 9–12 ranked taxa within each sampling period (Table 5).

TABLE 4.—Ichthyoplankton species collected in July-September samples off northern Chile (18°–24°S, 70°–72°W), 1964–83. Relative abundance (ROA) and percentage composition based on summed cruise mean abundances (no./10 m²) of all identified forms. Frequency is number of total 10 sampling periods when taxon was caught. Categories are PL (commercially important pelagic species) and other taxonomic components (M = myctophids; OM = other mesopelagic taxa; C = coastal forms).

Taxon	ROA	%	Frequency	Category
Engraulis ringens	1	74.29	9	PL
Sardinops sagax	2	9.33	10	PL
Normanichthys crockeri	3	3.36	9	C
Diogenichthys laternatus + *D. atlanticus*	4	2.90	10	M
Lampanyctus parvicauda	5	2.79	10	M
Triphoturus mexicanus	6	1.97	10	M
Bathylagus nigrigenys	7	1.44	10	OM
Trachurus murphyi	8	1.23	9	PL
Vinciguerria lucetia	9	1.04	10	OM
Blenniid D	10	0.43	9	C
Scomber japonicus	11	0.23	2	PL
Myctophum nitidulum	12	0.14	7	M
Unid. 1	13	0.13	3	C
Unid. 2	14	0.11	3	C
Hygophum bruuni	15	0.075	4	M
Diaphus sp.	16	0.062	5	M
Hygophum atratum	17	0.060	1	M
Sebastes sp.	18	0.050	5	C
Blenniid A	19	0.034	4	C
Ethmidium maculatum	20.5	0.030	1	PL
Merluccius gayi	20.5	0.030	2	PL
Unid. 3	22	0.028	4	C
Melamphaes sp.	23.5	0.026	3	OM
Gobiesocid A	23.5	0.026	4	C
Lampanyctus spp.	25	0.024	3	M
Sternoptyx diaphana	26	0.020	3	OM
Stomias spp.	27	0.017	1	OM
Blenniid C	28.5	0.016	2	C
Ophidiid	28.5	0.016	2	C
Beryciform	30	0.012	1	OM
Macrourid A	31	0.011	2	
Lestidiops pacificum	32.5	0.009	2	OM
Unid. 4	32.5	0.009	2	C
Melelectrona ventralis	34	0.008	1	M
Gadiform D	35	0.007	1	
Macrourid C	36	0.004	1	
Blenniid B	37.5	0.0036	1	C
Gobiesocid B	37.5	0.0036	1	C
Chauliodus sp.	39.5	0.0030	1	OM
Hippoglossina sp.	39.5	0.0030	1	C
Total number of identified larvae:		23,487		
Total number of samples:		576		
Total number of taxa:		41		

INTERANNUAL VARIATIONS IN ABUNDANCE AND COMPOSITION

The ichthyoplankton demonstrated extreme interannual variations in abundance and composition (Tables 3, 5; Fig. 3A, B). Most obvious are the 1) total larval and PL abundance peaks of 1966, 1972, and 1973 and 2) shift from anchoveta to sardine dominance between 1973 and 1983. The maximum total larval abundance values in 1966, 1972, and 1973 were 2.4–30 × higher than those of other years; the PL had 3–71 × higher abundances during these vs. other years. Interannual abundance variations during the seven years of lower abundance were also large for total larvae (to 6.9 ×) and the PL (to 12.7 ×). Anchoveta dominated the ichthyoplankton through 1973 (29.0–88.8%) and was directly responsible for the extreme abundance variations; anchoveta were absent from the 1983 samples, and sardine larvae (72.0%) contributed to the moderately high total larval and PL abundances (Table 5).

The OL fraction had less extreme abundance variations than the PL: maximum 1966, 1972, 1973, and 1983 mean abundance values ranged from 1.4 to 9× those of the other years; mean values within the six years of lower abundance varied to 3.8×. Unlike the PL, OL abundance fluctuations were not attributed to any one taxonomic component (Fig. 3B): the 1966 peak was largely due to coastal taxa (73% of OL); myctophids and other mesopelagic taxa equally dominated the 1972 peak (48%); myctophids dominated (79%) in 1983; and all three components were relatively abundant (29–40%) in 1973. Myctophids were generally the dominant component (50–90%) during the six years of lower OL abundance. Abundance fluctuations (as range of mean abundance values) across the 10 years were less extreme for myctophids (8.1 ×) than for the other mesopelagic taxa (32.3×) and coastal forms (160 ×).

In contrast to the ichthyoplankton, July–September zooplankton biomass values were relatively constant between years and exhibited only a 4× range in values (Table 3).

Despite large between-year variability in relative proportions of the PL and OL, there is a significant agreement of their ranked mean abundances across the 10 years ($\rho = +0.81$, $P < 0.01$). There is also a general agreement of the ranked mean abundances of PL and the three OL components across the 10 years ($W = 0.44$; $P = 0.05$). These categories were generally more abundant

TABLE 5.—Comparisons of relative abundances of dominant larval fish taxa collected off of northern Chile (18°–24°S, 70°–72°W) during July-September sampling periods, 1964–83. Relative abundances within each year are presented as (A) percentage contribution to total identified larvae and (B) ranked abundance. Taxa are listed in order of total summed 10-yr mean abundances.

Taxon	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
A. Percentage contribution to total identified larvae										
Engraulis ringens	71.89	28.99	88.76	57.32	52.20	54.05	87.69	70.35	87.70	—
Sardinops sagax	1.26	4.03	0.32	1.17	15.23	7.41	0.20	14.09	2.52	72.01
Normanichthys crockeri	4.09	1.18	7.18	1.43	1.66	7.91	1.41	0.10	1.52	—
Diogenichthys spp.	1.48	14.93	0.37	7.78	5.27	4.34	3.03	2.55	1.90	13.82
Lampanyctus parvicauda	9.76	25.28	1.68	16.07	7.80	11.48	0.81	1.28	0.58	1.88
Triphoturus mexicanus	7.57	12.48	0.53	7.40	3.32	9.43	1.61	0.85	1.14	4.07
Bathylagus nigrigenys	0.95	4.03	0.17	2.47	4.48	0.27	1.02	2.44	1.69	3.81
Trachurus murphyi	0.62	5.61	0.28	0.79	0.29	2.02	0.81	4.32	0.10	—
Vinciguerria lucetia	0.74	0.32	0.07	1.56	2.24	0.77	3.03	2.36	0.90	0.45
Blenniid D	1.26	0.32	0.43	1.81	3.03	0.77	—	0.12	0.42	0.12
Scomber japonicus	—	0.32	—	—	—	—	—	1.12	—	—
Myctophum nitidulum	0.10	—	0.01	—	0.29	0.27	—	0.21	0.21	0.56
Unid. 1	—	—	—	—	0.56	—	—	—	0.27	0.96
Unid. 2	—	—	0.01	—	—	—	—	0.01	0.57	—
Hygophum bruuni	—	2.21	0.03	0.92	—	—	—	—	—	0.11
Diaphus sp.	—	0.32	0.01	—	—	—	0.20	0.01	—	0.54
Hygophum atratum	—	—	—	—	—	—	—	—	—	0.81
Sebastes sp.	0.10	—	0.06	0.26	0.58	—	—	—	0.03	—
Other taxa	0.19	—	0.09	1.02	3.03	1.28	0.20	0.19	0.43	0.78
B. Ranked within-year abundance										
Engraulis ringens	1	1	1	1	1	1	1	1	1	—
Sardinops sagax	6.5	6.5	7	9	2	5	10	2	2	1
Normanichthys crockeri	4	9	2	8	9	4	5	12	5	—
Diogenichthys spp.	5	3	6	3	4	6	2.5	4	3	2
Lampanyctus parvicauda	2	2	3	2	3	2	7.5	7	8.5	5
Triphoturus mexicanus	3	4	4	4	6	3	4	9	6	3
Bathylagus nigrigenys	8	6.5	9	5	5	12.5	6	5	4	4
Trachurus murphyi	10	5	8	11	17	7	7.5	3	13.5	—
Vinciguerria lucetia	9	11.5	10	7	8	9	2.5	6	7	10
Blenniid D	6.5	11.5	5	6	7	9	—	11	10	13.5
Scomber japonicus	—	11.5	—	—	—	—	—	8	—	—
Myctophum nitidulum	12.5	—	18.5	—	17	12.5	—	10	12	8
Unid. 1	—	—	—	—	12.5	—	—	—	11	6
Unid. 2	—	—	18.5	—	—	—	—	20.5	8.5	—
Hygophum bruuni	—	8	12	10	—	—	—	—	—	15.5
Diaphus sp.	—	11.5	18.5	—	—	—	10	20.5	—	9
Hygophum atratum	—	—	—	—	—	—	—	—	—	7
Sebastes sp.	12.5	—	11	13.5	14	—	—	—	21	—

in 1966, 1972, and 1973 and relatively rare in 1965 and 1968. The ranked abundance patterns of each of the components differ from one another (e.g., all pairwise correlation coefficients [$\rho = -0.21$ to $+0.61$] are nonsignificant). Larval diversity is strongly correlated with total larval abundance ($\rho = +0.88$, $P < 0.01$).

There are no significant correlations between abundance ranks of invertebrate zooplankton biomass and total larvae ($\rho = +0.27$) or any of the larval categories ($\rho = -0.03$ to $+0.22$; $P > 0.05$ in all cases).

Species Abundance Variations and Relations

The top 10 ranking larval fish taxa were caught during at least 9 of the 10 sampling periods (Table 4). All of these taxa exhibited large interannual abundance fluctuations (Table 3). Most marked were the abundance changes of anchoveta, sardine, and coastal species *Normanichthys crockeri*. This latter species (rank 3 in overall abundance) was frequently abundant prior to 1983; like anchoveta it was absent from 1983 samples. Among the 10 taxa only *Triphoturus mexicanus* had <10× changes in mean abundance values; <20× changes occurred for *Lampanyctus parvicauda* (11.5×) and *Diogenichthys* spp. (18.4×); all other taxa had >20× mean abundance changes over the 10 years. The abundance fluctuations of these 10 taxa are primarily responsible for the interannual abundance and composition variations (Table 5; Fig. 3A, B).

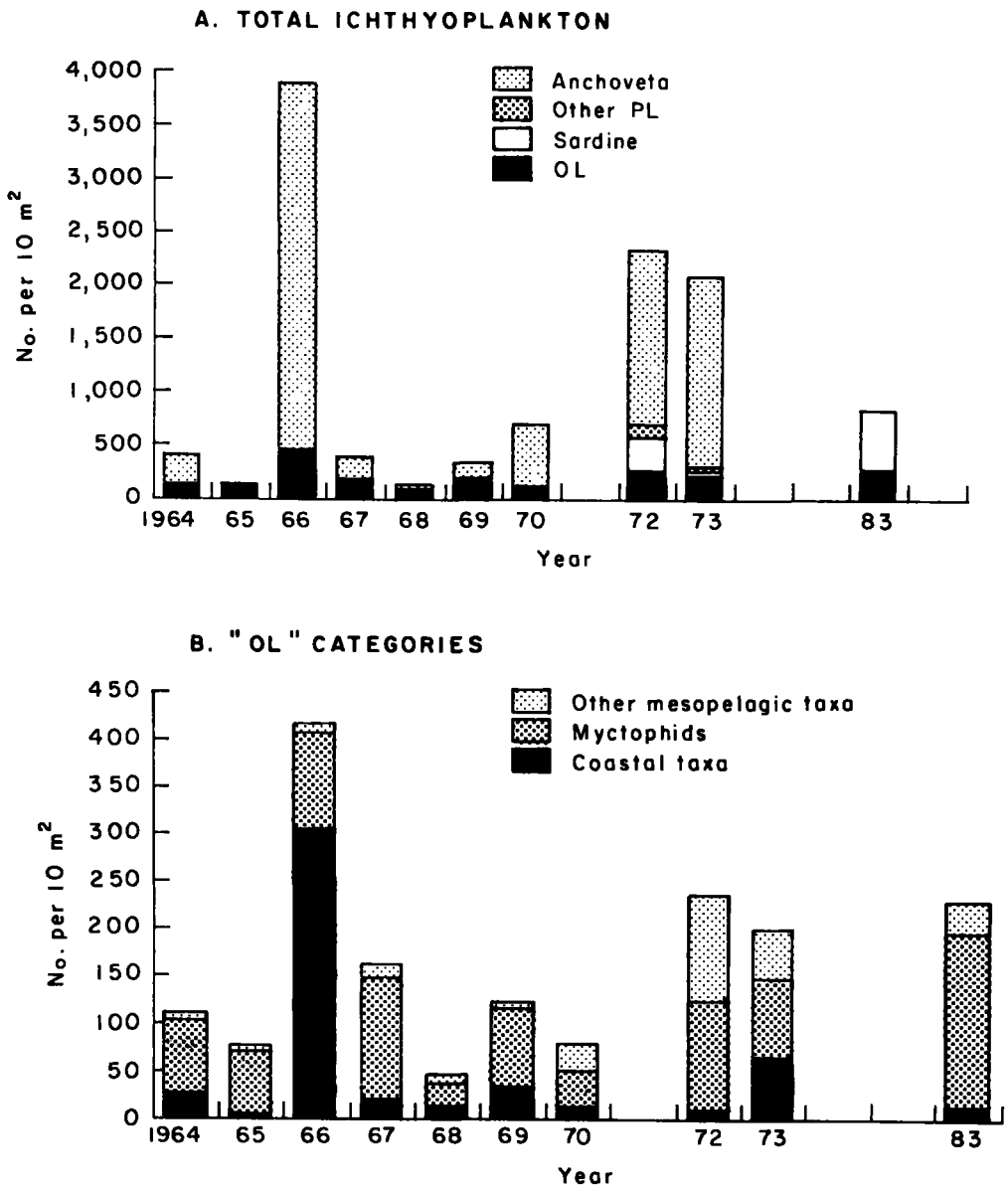

FIGURE 3.—Mean abundance (numbers per 10 m^2) of (A) total ichthyoplankton and major PL components and (B) total OL and major OL components collected off northern Chile (18°–24°S) during July–September sampling periods, 1964–83.

Between-year comparisons of the species percentage compositions of total larvae give a wide range of PSI values (3.3–95.0; Table 6A) which primarily reflect similarity in percentages of anchoveta; 51% of these values are moderate to high (e.g., ≥65). Highest values (91.5–95.0) come from comparisons between 1966, 1970, and 1973 when anchoveta contributed >87% of the larvae. High values (80.7–82.5) also result from comparisons between 1964, 1967, and 1969 and result from moderate anchoveta abundance (54.0–71.9%) and relatively similar proportions of other taxa. Lowest values (3.3–31.0) result from comparisons of 1983 vs. all other years and reflect the absence of anchoveta larvae in 1983 samples. The 1973 and 1983 PSI values are little affected (e.g., ≤2.3) by

TABLE 6.—Between-year percent similarity index (PSI) values from comparisons of (A) total larvae and (B) the OL (other larval taxa) fraction collected during July–September sampling periods off northern Chile (18°–24°S), 1964–83.

	PSI values for								
	1965	1966	1967	1968	1969	1970	1972	1973	1983
A. Total larvae									
1964	52.44	79.94	82.22	71.25	80.70	79.70	77.89	80.30	10.30
1965	X	33.95	67.41	55.54	62.38	38.16	45.32	38.74	28.47
1966		X	62.69	57.83	65.08	91.55	73.65	91.88	3.32
1967			X	77.96	82.47	67.75	68.21	66.82	18.05
1968				X	79.39	62.81	76.39	63.68	30.95
1969					X	62.95	69.67	63.50	18.80
1970						X	79.06	94.95	7.31
1972							X	79.42	22.02
1973								X	8.95
B. OL fraction									
1964	69.88	47.01	75.76	57.56	85.16	45.99	36.08	51.29	33.15
1965	X	29.22	88.07	60.36	68.42	55.43	54.30	47.13	54.39
1966		X	34.96	36.78	50.09	30.53	26.15	37.50	18.48
1967			X	70.21	71.01	53.92	52.55	55.68	49.12
1968				X	58.46	54.85	61.57	67.92	51.92
1969					X	48.98	39.22	51.92	37.18
1970						X	74.35	68.40	60.21
1972							X	66.23	58.74
1973								X	58.61

accommodations for possible sampling depth-catch differences of *Trachurus gayi* and *Triphoturus mexicanus*.

When the PL are excluded, comparisons between the OL taxa yield generally lower PSI values than those of the total larvae; only 24% of the 18.5–88.1 values are moderate to high (Table 6B). Moderate to high values (69.9–88.1) come from comparisons between 1964, 1965, 1967, and 1969, and in part result from similar proportions of *Lampanyctus parvicauda* (32.1–41.4%) and *Triphoturus mexicanus* (18.2–28.9%) during those years. Moderate values (66.2–74.4) also come from comparisons of 1967 vs. 1968 and 1969 (similar proportions of *L. parvicauda*, *T. mexicanus*, and *Diogenichthys* [12.2–39.5%]); 1970 vs. 1972 (similar proportions of *Vinciguerria lucetia* and *Diogenichthys* [23.4–26.8%]); and 1972 vs. 1973 (similar proportions of *Bathylagus nigrigenys*, *V. lucetia*, and *Diogenichthys* [9.3–25.3%]). Lowest PSI values (<30) result from comparisons of 1966 vs. 1965, 1970, 1972, and 1983, and are due largely to extreme dominance by *Normanichthys crockeri* (67.4% of OL) in 1966. Recalculations to accommodate for possible depth-related increased catches of *T. mexicanus* in most cases decrease 1973 and 1983 PSI values (e.g., by 2.6–7.2) and in two cases (1968 and 1970 vs. 1973) change the value characterization from moderate (67.9 and 68.4) to low (63.8 and 64.5). With one exception (1972 vs. 1973, PSI = 67.0) all of the other adjusted values are low.

Species Across-Year Ranked Abundance Patterns

Individual species across-year abundance rankings demonstrate a variety of patterns. Three patterns are shared by nine of the more frequently occurring taxa (Table 7). These involve 1) a group formed by anchoveta and three coastal forms; 2) a group formed by one myctophid and two other mesopelagic species; and 3) a species pair consisting of sardine and a myctophid. Another species pair (two myctophids) can be formed if the 1973 and 1983 abundances of *T. mexicanus* are adjusted.

Group I includes anchoveta, *Normanichthys crockeri*, Blenniid D, and *Sebastes* sp. (Table 7). There is a significant concordance among these species as to years of highest (1966 and 1973) and lowest (1965 and 1983) abundance ($W = 0.69$, $P < 0.01$). The abundance rankings of anchoveta and *N. crockeri* ($\rho = +0.79$) and of Blenniid D and *Sebastes* ($\rho = +0.88$) are significantly correlated ($P \leq 0.01$). None of the correlations between species of the two pairs are significant due to differences in 1967–68 vs. 1970–72 relative abundances.

The three Group II species, *Diogenichthys later-*

natus, *Bathylagus nigrigenys*, and *Vinciguerria lucetia*, have a concordance of higher abundances in 1972, 1973, and 1983 vs. other years ($W = 0.81$, $P < 0.01$). The abundance rankings of *B. nigrigenys* are strongly correlated with those of *D. laternatus* and *V. lucetia* ($\rho = +0.82$, $P < 0.01$ in both cases); the correlation between *D. laternatus* and *V. lucetia* is not significant.

The abundance rankings of sardine and *Myctophum nitidulum* (Pair I species) are significantly correlated ($\rho = +0.96$, $P < 0.01$); both species were rare or absent in 1970 and most abundant in 1972, 1973, and 1983.

With adjustment to 1973 and 1983 abundances of *T. mexicanus*, its abundance rankings are strongly correlated with those of *Lampanyctus parvicauda* (Pair II species; $\rho = +0.84$, $P < 0.01$). Highest relative abundances of both species were in 1964, 1966, 1967, and 1969.

Three relatively frequent species (*Trachurus murphyi*, *Diogenichthys atlanticus*, and *Diaphus* sp.) do not conform to any of the above patterns. If the 1973 *Trachurus* abundance is adjusted to accommodate for possible undersampling, its abundance pattern is similar to that of anchoveta ($\rho = +0.68$, $P = 0.05$) but not to any of the other Group I species ($\rho = +0.03$ to $+0.46$).

VARIATIONS IN ABUNDANCE AND COMPOSITION RELATIVE TO HYDROGRAPHIC CONDITIONS

Ichthyoplankton abundances in the 10 years sampled show no consistent patterns relative to warm water-cold water events (Table 8). High PL and OL abundances occurred during strong El Niño events (1972 and 1983) and during cold or transition years immediately following El Niños (1966 and 1973). Lowest abundances of both fractions were associated with the 1965 El Niño and warm 1968. Neither the PL nor OL have significant correlations with ranked (high to low) July–

TABLE 7.—Larval fish taxa grouped according to similar across-year (1964–83) ranked abundance patterns. Significant agreement of group rankings indicated by Kendall's concordance (W) values. Correlations between species pair rankings indicated by Spearman's rho (ρ) values. Significant values at $P \leq 0.05$ are indicated, but note use of multiple testing. ** = abundance ranks adjusted to accommodate for possible sampling depth related catch differences (Table 2).

	Abundance rank for									
Species	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Group I										
Engraulis ringens	5	9	1	6	8	7	4	3	2	10
Normanichthys crockeri	4	9	1	6	8	3	5	7	2	10
Blenniid D	4	9	1	3	5	7	10	6	2	8
Sebastes sp.	5	8	1	2	3	8	8	8	4	8
		W = 0.69 ($P < 0.01$)								
E. ringens-N. crockeri		ρ = +0.79 (P = 0.01)								
Blenniid D-*Sebastes* sp.		ρ = +0.88 ($P < 0.01$)								
E. ringens-Blenniid D		ρ = +0.59								
E. ringens-Sebastes sp.		ρ = +0.44								
N. crockeri-Blenniid D		ρ = +0.61								
N. crockeri-Sebastes sp.		ρ = +0.48								
Group II										
Diogenichthys laternatus	10	5	7.5	4	9	7.5	6	2	3	1
Bathylagus nigrigenys	9	8	6	4	7	10	5	1	2	3
Vinciguerria lucetia	6.5	10	8	4	6.5	9	2	1	3	5
		W = 0.81 ($P < 0.01$)								
B. nigrigenys-D. laternatus		ρ = +0.82 ($P < 0.01$)								
B. nigrigenys-V. lucetia		ρ = +0.82 ($P < 0.01$)								
D. laternatus-V. lucetia		ρ = +0.52								
Pair I										
Sardinops sagax	7	8	6	9	5	4	10	2	3	1
Myctophum nitidulum	6	9	6	9	6	4	9	1	3	2
S. sagax-M. nitidulum		ρ = +0.96 ($P < 0.01$)								
Pair II										
Lanpanyctus parvicauda	3	5	1	2	9	4	10	6	8	7
*Triphoturus mexicanus***	1	6	4	3	10	2	8	5	9	7
*L. parvicauda-T. mexicanus***		ρ = +0.84 ($P < 0.01$)								

TABLE 8.—Range, mean, standard deviation and ranked (high to low) values of sea ichthyoplankton sampling periods, 1964–83. N = number of observations. N.A. = data not (1976), Bernal et al. (1982), and Kelly and Blanco (1983).

	1964	1965	1966	1967	1968
Temperature (°C)					
N	85	128	72	55	81
Range	13.5–17.9	13.6–18.1	13.7–17.1	13.3–16.0	14.3–18.6
$\bar{X}$	15.7	16.5	15.3	14.8	16.5
(S)	(1.0)	(1.0)	(0.8)	(0.8)	(0.9)
Rank	7	3.5	8	9	3.5
Salinity (‰)					
N	84	124	72	4	81
Range	34.51–34.99	34.80–35.40	34.53–35.03	34.74–34.82	34.69–35.23
$\bar{X}$	34.74	35.06	34.83	34.78	34.92
(S)	(0.12)	(0.12)	(0.11)	(0.04)	(0.12)
Rank	9	2	6	8	4
Hydrographic condition:	Cold	El Niño	Transition	Cold	Warm

September mean temperature and salinity values; larval diversity (mean number of taxa/tow) also shows no correlation with these values (Table 9). Within the PL, anchoveta were most abundant during years immediately following El Niños (cold 1966, transition 1973), the 1972 El Niño, and cold 1970; lowest abundances were during the 1965 and 1983 El Niños (Table 8). There are no significant correlations between ranked anchoveta abundances and ranked values of temperature or salinity (Table 10). Sardine larvae were most abundant during and after the 1972 El Niño; prior to this moderate abundances and relatively large percentage contributions to the ichthyoplankton occurred only during the warm 1968–69 period (Tables 5, 7). Lowest sardine abundances were during cold years 1964, 1967, and 1970 and the 1965 El Niño. Despite low abundances during the 1965 El Niño, there is a significant positive correlation between ranked sardine abundance and temperature ($\rho = +0.69$, $P < 0.05$). Ranked larval anchoveta and sardine abundances are not correlated ($\rho = -0.07$).

The only apparent warm-cold year abundance pattern among the OL categories is that of the coastal taxa; this group had lowest abundances during the 1965, 1972, and 1983 El Niños and highest abundances in subsequent 1966 and 1973 transition years. The ranked abundance pattern of this category has negative correlations ($P \leq 0.05$) with ranked temperature ($\rho = -0.69$) and salinity ($\rho = -0.68$) values (Table 9). Both the myctophid and other mesopelagic categories appear to have abundance patterns unrelated to warm-cold hydrographic conditions (Table 9).

TABLE 9.—Correlations of across-year abundance ranks of zooplankton and ichthyoplankton categories with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods off northern Chile, 1964–83. Correlations based on Spearman's rho tests. Significant values at $P \leq 0.05$ are indicated, but note use of multiple testing. PL = larvae of pelagic species; OL = other larval taxa.

	Temperature (°C)		Salinity (‰)	
Zooplankton	−0.48		−0.37	
PL	−0.10		−0.17	
OL	−0.02		+0.05	
Larval diversity: (mean no. taxa/tow)	+0.12		0.00	
Myctophids	+0.02		+0.12	
Other mesopelagic taxa	+0.28		+0.12	
Coastal taxa	−0.69	$P < 0.05$	−0.68	$P = 0.05$

Zooplankton biomass values show negative but nonsignificant correlations with temperature and salinity (Table 9). This is in agreement with the time-series analysis results of Bernal et al. (1983) which demonstrated no consistent relations of zooplankton biomass with cold- or warm-water events.

Species Groups and Hydrographic Conditions

The species groups formed by similarity of between-year abundance ranks demonstrate both positive and negative correlations with cold- and warm-year conditions (Table 10). Group I and Pair II and their member species have negative correlations with ranked temperature and salinity values indicating a tendency for higher

surface temperature (°C) and salinity (‰) values during July–September available. Hydrographic "condition" descriptions for these periods are from Robles et al.

	1969	1970	1972	1973	1983
Temperature (°C)					
N	35	N.A.	110	43	24
Range	14.6–17.5		15.5–18.5	14.3–17.4	15.1–19.0
$\bar{X}$	16.0		17.2	15.8	17.2
(S)	(1.0)		(0.7)	(0.9)	(0.9)
Rank	5		1.5	6	1.5
Salinity (‰)					
N	35	N.A.	108	43	20
Range	34.60–35.19		34.75–35.96	34.60–35.13	34.81–35.39
$\bar{X}$	34.87		35.05	34.82	35.09
(S)	(0.16)		(0.18)	(0.13)	(0.19)
Rank	5		3	7	1
Hydrographic condition:	Warm	Cold	El Niño	Transition	El Niño

TABLE 10.—Correlations of across-year abundance ranks of larval fish species groups and member species with ranked (high to low) mean temperature and salinity values from nine July–September sampling periods, 1964–83. Correlations based on Spearman's rho tests. Group correlations based on ranks of summed within-year ranks of member species. Significant values at $P \leq 0.05$ are indicated but note use of multiple testing. ** = abundance ranks adjusted to accommodate for apparent large sampling depth-related catch differences.

Species	Temperature (°C)	Salinity (‰)
Group I	−0.78 $P < 0.05$	−0.78 $P < 0.05$
Engraulis ringens	−0.52	−0.62
Normanichthys crockeri	−0.69 $P < 0.05$	−0.72 $P < 0.05$
Blenniid D	−0.74 $P < 0.05$	−0.77 $P < 0.05$
Sebastes sp.	−0.67	−0.55
Group II	+0.27	+0.20
Diogenichthys laternatus	+0.45	+0.50
Bathylagus nigrigenys	+0.27	+0.20
Vinciguerria lucetia	+0.12	−0.14
Pair I	+0.70 $P < 0.05$	+0.49
Sardinops sagax	+0.69 $P < 0.05$	+0.50
Myctophum nitidulum	+0.61	+0.35
Pair II	−0.62	−0.57
Lampanyctus parvicauda	−0.68 $P = 0.05$	−0.48
*Triphoturus mexicanus***	−0.50	−0.53

abundances during colder, lower salinity periods. The rankings of Group I (based on ranks of summed within-year member species ranks) are significantly correlated ($P < 0.05$) with both temperature and salinity ($\rho = -0.78$ in both cases). Within this group the rankings of *Normanichthys crockeri* and Blenniid D are correlated ($P < 0.05$) with temperature and salinity ($\rho = -0.69$ to -0.77); the correlation of *Sebastes* with temperature is also relatively strong ($\rho = -0.67$). Within Species Pair II, *Lampanyctus parvicauda* abundance has a relatively strong negative correlation with temperature ($\rho = -0.68$).

Group II and Pair I and their member species have positive correlations of ranked abundance with temperature and (with one exception) salinity values (Table 10) suggesting a tendency for higher abundances during warmer, higher salinity conditions. These correlations are all non-significant and generally weak for Group II and its member species (*Bathylagus nigrigenys*, *Vinciguerria lucetia*, and *Diogenichthys laternatus*). Pair I has a positive correlation ($P < 0.05$) with temperature ($\rho = +0.70$) primarily due to sardine abundance ranks.

Species Percentage Composition Relative to Hydrographic Conditions

Ichthyoplankton percentage composition shows no striking warm year vs. cold year related patterns. Total ichthyoplankton composition comparisons between years of "similar" hydrographic conditions do not give overall higher PSI values than do comparisons between years of different conditions (Table 11A). PSI values (ranges, means, and proportions of high and moderate values) from comparisons of cold, transition, and warm years are similar. However, highest values (91.6–94.9) come from cold vs. transition year (1970 vs. 1966 and 1973) and between-transition year (1966 vs. 1973) comparisons. Additionally, intercomparisons of the transition, warm, and El Niño years give relatively lower values than do cold-year comparisons. Comparisons between El Niño years give generally PSI low values.

TABLE 11.—Within- and between-hydrographic period ichthyoplankton composition comparisons presented as range, mean, and standard errors of percent similarity index (PSI) values and numbers (N) out of total comparisons having moderate to high (e.g., ≥65) values. A. Total larvae. B. OL (other larval taxa) fraction.

		PSI values for			
		Cold	Transition	Warm	El Niño
A. Total larvae					
Cold years	Range	67.8–82.2	62.7–94.9	62.8–82.5	7.3–79.1
(1964, 1967, 1970)	$\bar{X}$	76.6	79.4	73.0	46.5
	(SE)	(4.5)	(5.2)	(3.6)	(9.6)
	N	3/3	5/6	4/6	4/9
Transition years	Range			57.8–65.1	3.3–79.4
(1966, 1973)	$\bar{X}$		91.9	62.5	39.7
	(SE)			(1.6)	(12.9)
	N		1/1	1/4	2/6
Warm years	Range				18.8–76.4
(1968, 1969)	$\bar{X}$			79.4	52.3
	(SE)				(9.2)
	N			1/1	2/6
El Niño years	Range				22.0–45.3
(1965, 1972, 1983)	$\bar{X}$				31.9
	(SE)				(7.0)
	N				0/3
B. OL					
Cold years	Range	46.0–75.8	30.5–68.3	47.0–85.2	33.2–88.1
(1964, 1967, 1970)	$\bar{X}$	58.6	48.0	64.6	57.6
	(SE)	(8.9)	(5.7)	(5.4)	(5.9)
	N	1/3	1/6	3/6	3/9
Transition years	Range			36.8–67.9	18.5–66.2
(1966, 1973)	$\bar{X}$		37.5	51.7	41.0
	(SE)			(6.4)	(7.8)
	N		0/1	1/4	1/6
Warm years	Range				37.2–68.4
(1968, 1969)	$\bar{X}$			58.5	53.1
	(SE)				(5.2)
	N			0/1	1/6
El Niño years	Range				54.3–58.7
(1965, 1972, 1983)	$\bar{X}$				55.8
	(SE)				(1.5)
	N				0/3

The OL percentage composition similarly does not demonstrate clear hydrographically related patterns (Table 11B). As with the total larvae, comparisons of cold vs. other years yield most of the moderate to high PSI values. Highest values (88.1 and 85.2) come from comparisons of cold vs. El Niño (1965 vs. 1967) and cold vs. warm (1964 vs. 1969) years. Comparisons within and between transition, warm and El Niño years give primarily low values. Recalculation of PSIs to accommodate for *Triphoturus mexicanus* lowers mean values for comparisons with 1973 and 1983 by only 0.4–2.3 and does not affect the overall results.

Chronological Considerations of Species Composition

When the total larval and OL PSI data are considered in terms of chronological rather than hydrographic periods, various patterns become apparent (Table 12). For the total ichthyoplankton, comparisons within the 1964–69 data set and between this and the 1970–73 data set give similar means, ranges, and proportions of moderate to high values. In contrast, comparisons within the 1970–73 data set provide more similar values and a significantly higher mean value than results from comparisons within the 1964–69 set (Z test, $P < 0.01$). This suggests that, despite the varied hydrographic conditions represented during the 1970–73 period, conditions were favorable for a repeated fairly similar anchoveta-dominated ichthyoplankton assemblage during July–September months.

Chronologically grouped comparisons of the OL fraction provide somewhat different patterns from those of the total ichthyoplankton (Table 12B) and indicate a marked change in species

proportions between 1964–69 and later years. Comparisons within the 1964–69 OL data set yield all of the high and most of the moderate PSI values. The mean PSI value from these comparisons is significantly higher ($P < 0.05$) than that from 1964–69 vs. 1970–73 comparisons. As with the total larvae, the 1970–73 PSI values are similar and moderately high and the 1983 comparison values are relatively low compared with other years. Accommodation for *T. mexicanus* abundance reduces slightly (1.1–3.1) the mean values from comparisons with 1970–73 and 1983 data sets and strengthens the significance of difference ($P < 0.01$) between 1964–69 and 1964–69 vs. 1970–73 mean values.

The difference in OL PSI values between 1964–69 and 1970–83 is, to a great extent, due to abundance shifts of Group II and Pair II species. The abundance ranks of all three Group II species (Table 7) indicate significantly higher abundances during 1970–83 than in earlier years (Man Whitney U tests, all P's ≤ 0.05). Additionally, the averaged abundance estimates from these four years are significantly higher than from earlier years (Z tests; $P < 0.01$ for *Bathylagus nigrigenys* and *Vinciguerria lucetia*, $P < 0.05$ for *Diogenichthys* spp.). Together *B. nigrigenys*, *V. lucetia*, and *Diogenichthys* spp. (primarily *D. laternatus*) contributed 46.5–72.8% of the OL collected during 1970–83 compared with 5.8–37.1% during 1964–69 (Table 13).

In contrast, Pair II species *Lampanyctus parvicauda* and *Triphoturus mexicanus* were relatively less abundant during 1970–83 than in previous years. These two species contributed 21–66% of the OL during 1964–69 compared with <22% during 1970–83 (Table 13). With adjustments to *T. mexicanus* abundance these species proportions in 1973 and 1983 decrease to 11.8% and 13.2%, and those of the Group II species increase to 49.9% and 71.4%, respectively. The relative abundance decrease of Pair II was primarily

TABLE 12.—Within- and between-time period ichthyoplankton composition comparisons presented as ranges, means, and standard errors of percent similarity index (PSI) values and numbers (N) out of total comparisons having moderate to high (e.g., ≥65) values. A. Total larvae. B. OL (other larval taxa) fraction.

		PSI values for		
		1964–69	1970–73	1983
A. Total larvae				
1964–69	Range	33.9–82.5	38.2–91.9	3.3–31.0
	$\bar{X}$	67.4	67.7	18.2
	(SE)	(3.6)	(3.6)	(4.3)
	N	9/15	11/18	0/6
1970–73	Range		79.1–95.0	7.3–22 0
	$\bar{X}$		84.4	12.8
	(SE)		(5.2)	(4.7)
	N		3/3	0/3
B. OL				
1964–69	Range	29.2–88.1	26.2–67.9	18.5–54.4
	$\bar{X}$	60.2	48.4	40.7
	(SE)	(4.6)	(2.5)	(5.6)
	N	7/15	1/18	0/6
1970–73	Range		66.2–74.4	58.6–60 2
	$\bar{X}$		69.7	59.2
	(SE)		(2.4)	(0.5)
	N		3/3	0/3

TABLE 13.—Percentage contribution by dominant OL (other larval taxa) species collected during July–September sampling periods, 1964–83. Species arranged according to group affiliations based on across-year ranked abundance patterns.

	Percentage contribution for									
	1964	1965	1966	1967	1968	1969	1970	1972	1973	1983
Group I										
Normanichthys crockeri	15.61	1.94	67.40	3.51	5.15	22.13	12.52	1.02	15.72	—
Sebastes sp.	0.36	—	0.60	0.63	1.79	—	—	—	0.35	—
Blenniid D	4.81	0.52	4.00	4.45	9.40	2.16	—	1.19	4.31	0.44
Group total	20.78	2.46	72.00	8.59	16.34	24.29	12.52	2.21	20.38	0.44
Group II										
Bathylagus nigrigenys	3.63	6.60	1.61	6.08	13.87	0.75	9.01	24.14	17.53	13.78
Vinciguerria lucetia	2.81	0.52	0.70	3.82	6.94	2.16	26.78	23.37	9.31	1.62
Diogenichthys spp.	5.63	24.45	3.50	19.11	16.33	12.15	26.78	25.29	19.68	49.96
Group total	12.07	31.57	5.81	29.01	37.14	15.06	62.57	72.80	46.52	65.36
Pair I										
Myctophum nitidulum	0.36	—	0.10	—	0.89	0.75	—	2.05	2.15	2.01
Pair II										
Lampanyctus parvicauda	37.21	41.40	15.77	39.47	24.16	32.11	7.13	12.67	6.06	6.78
Triphoturus mexicanus	28.86	20.44	4.99	18.17	10.29	26.37	14.27	8.40	11.82	14.70
Pair total	66.07	61.84	20.76	57.64	34.45	58.48	21.40	21.07	17.88	21.48

due to the increased numbers of Group II species and decreased numbers of *L. parvicauda*. The 1970–83 averaged abundance of *L. parvicauda* is significantly lower (Z test; $P < 0.01$) than that of 1964–69. *Triphoturus mexicanus* averaged abundance (both adjusted and unadjusted values) is similar ($P > 0.05$) between the two time periods.

DISCUSSION

The northern Chilean ichthyoplankton data set is obviously weakened by lack of information from the 1974–82 period; this missing information is critical for an appreciation of the temporal extent and relative constancy of the apparent ichthyoplankton composition change in 1970–73 vs. earlier years. This data set also suffers from limited seasonal coverage which prohibits examination of between-year variations in spawning time and intensity as a cause of interannual abundance fluctuations and apparent composition change. However, the existing data set does provide coherent coverage over varied hydrographic conditions between 1964 and 1973 and is sufficient to test for correlations with short-term (e.g., year to year) fluctuations in hydrographic conditions.

The large interannual changes in abundance and composition of the northern Chilean ichthyoplankton can to a certain extent be related to interannual changes of hydrographic conditions in the Humboldt Current. This has been demonstrated through correlations of ranked temperature and salinity values and abundances of coastal species, sardine, and *Lampanyctus parvicauda* (Tables 9, 10). The temperature and salinity values used in these correlation tests represent ambient conditions during the July–September spawning period and therefore possibly reflect only conditions affecting egg and early larval (e.g., to stages capable of substantial net avoidance) survival. These values do not necessarily reflect longer term conditions affecting abundance, distributions, and fecundities of adult populations or later larval survival and recruitment. However, there is a generally good correspondence between these values and reported longer term hydrographic conditions in the Humboldt Current over the 19-yr timespan (e.g., Table 8; Robles et al. 1976; Bernal et al. 1983; Guillén 1983; Bakun 1987).

Despite significant correlations between abundances of some ichthyoplankton components and temperature and salinity values, there is no apparent consistency of total larval or OL species percentage compositions during years of "similar" hydrographic conditions (Table 11). More coherent patterns emerge from considerations of the 1964–69 and 1970–73 data sets (Table 12). This chronological separation is also supported by the ranked abundance patterns of the various species groups and pairs (Table 7).

Among the least confusing across-year abundance patterns demonstrated by the ichthyoplankton are 1) generally greater abundance of Group II species after 1969, 2) greatest abundance of Pair I species after 1970, and 3) predominantly higher abundances of one of the Pair II species prior to 1970 (Table 7). Associated with the Group II and Pair II abundance patterns are large shifts in their relative proportions (Table 13).

The shift from relatively large percentage contributions by *Lampanyctus parvicauda* and *Triphoturus mexicanus* to larger proportions of *Diogenichthys* spp., *Bathylagus nigrigenys*, and *Vinciguerria lucetia* after 1969 is notable. The abundances of these mesopelagic species, unlike those of anchoveta and sardine, are not directly influenced by man's fishing activities and so may be interpreted as indicators of environmental change. Furthermore, the timing of these species absolute and relative abundance changes preceded by several years the dramatic changes in anchoveta and sardine stocks off of northern Chile (Fig. 4) and so cannot be directly related to biological consequences of change in the dominant pelagic schooling fish stocks.

Although fragmentary, there is evidence for a change in zooplankton biomass values off northern Chile (18°–24°S) occurring in 1969 (Fig. 5) which, like OL percentage composition, suggests a possible environmental change. Time series analysis of quarterly zooplankton biomass values during 1964–73 indicate generally lower biomass during 1969–73 relative to the 1964–68 period. As with total larval abundance (Table 9), these zooplankton biomass variations do not appear to be related to warm year-cold year events (Bernal et al. 1983).

The changes in OL composition and zooplankton biomass suggest that there was subtle but large-scale (low-frequency) environmental transition occurring in the 1969–70 period. Various indications of environmental change occurring about this time are present in long-term physical data bases from Chile and Peru. Predominantly

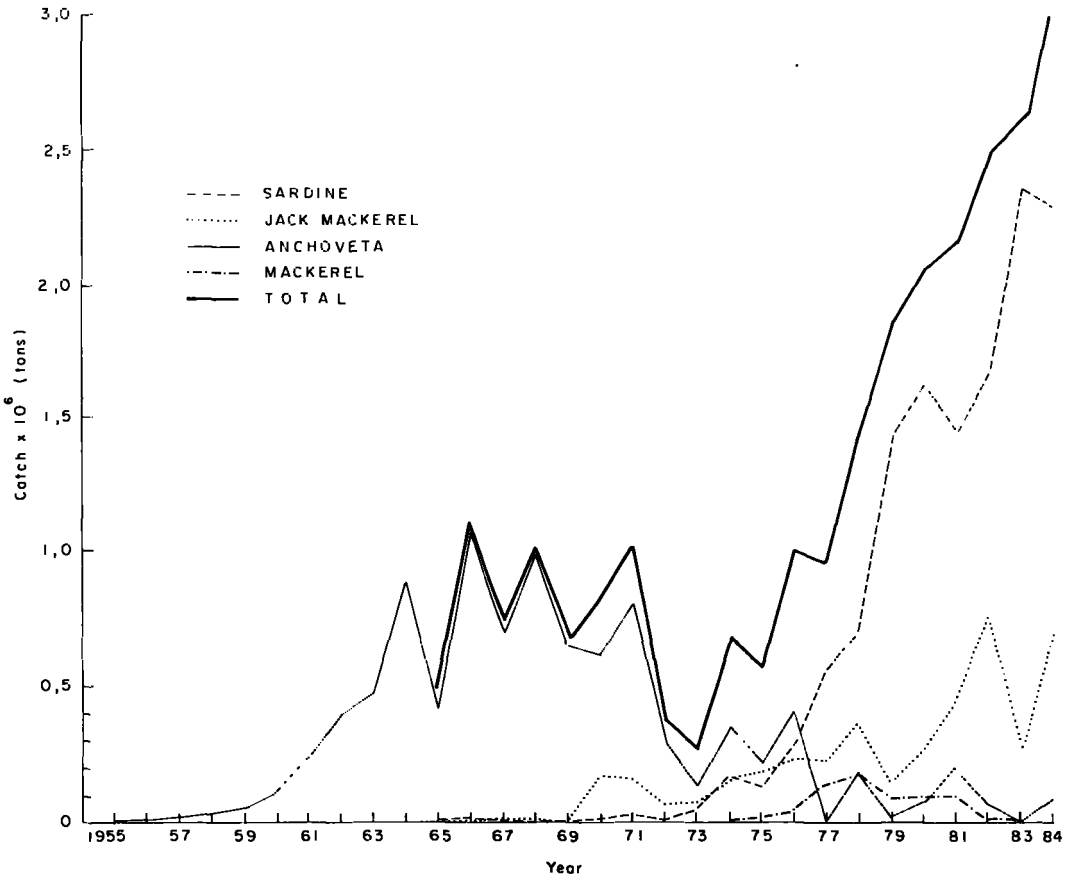

FIGURE 4.—Total catch and catch of dominant species taken in the northern Chilean pelagic fishery, 1955–84.

negative sea surface atmospheric pressure anomalies occurred off of Arica from 1960 to 1972 with a strong negative anomaly occurring in 1969; predominantly positive anomalies occurred there after 1972 (Fig. 6A). A similar but less extreme change from negative or neutral anomalies to predominantly positive anomalies occurred off Iquique (20°S) in 1970 (Fig. 6B; Kelly and Blanco 1983).

Off Peru (5°–15°S) the wind driven turbulent mixing index of surface waters shows a general increase during and after the 1972 El Niño event (Fig. 7A; Bakun 1987). A probable result of this increased turbulence is an increase in standard deviations associated with monthly temperature values; standard deviations above the 30-yr mean generally persisted throughout the year from 1972 to 1984 (Fig. 7B) and suggest increased physical variability and heterogeneity in this later period. Comparable data sets from northern Chile are not available to determine if these latter two features were also characteristic of the Chilean area.

How these observed atmospherically related changes could be related to changes in the marine environment off northern Chile is uncertain. It is possible that the observed changes in atmospheric pressure off Arica and Iquique have associated changes in advection of water mass and faunal sources. Bernal et al. (1983) discussed El Niño related changes in water mass distribution off Chile in 1972 and 1973 relative to cold-year 1967. These changes involved southerly extensions of oceanic subtropical and equatorial subsurface waters, strengthening of the spring-summer thermocline, and cessation of coastal upwelling. These authors did not examine water mass distributions in the 1968–70 period. However, lowered zooplankton biomass starting in 1969 and the OL composition change starting around 1970 suggest that the hydrographic conditions attributed to the 1972 El Niño may have been an intensification of

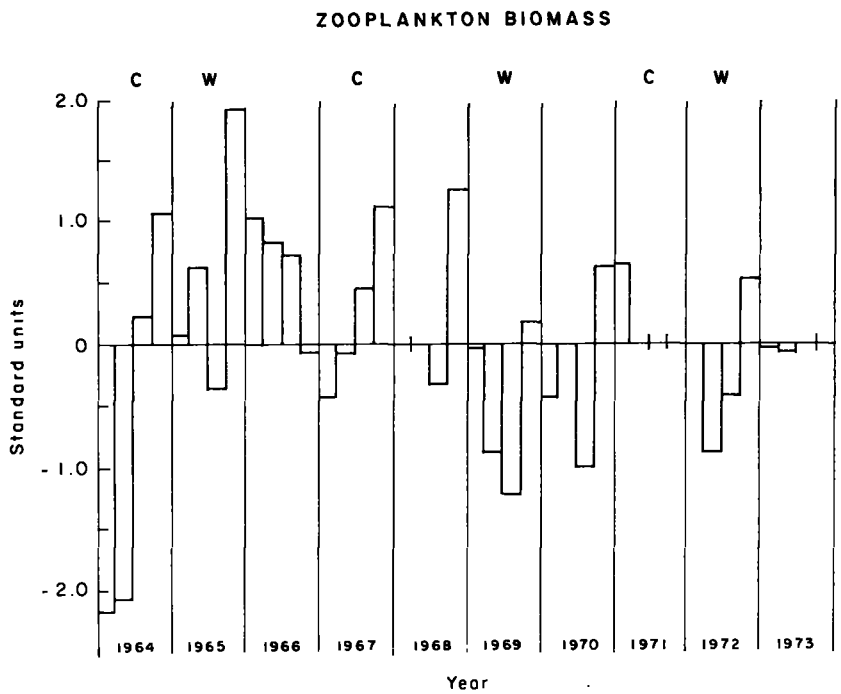

FIGURE 5.—Time series estimates of quarterly zooplankton biomass values from northern Chile (18°–24°S), 1964–73, standardized according to the long term standard deviation. W = warm years; C = cold years. From Bernal et al. 1983.

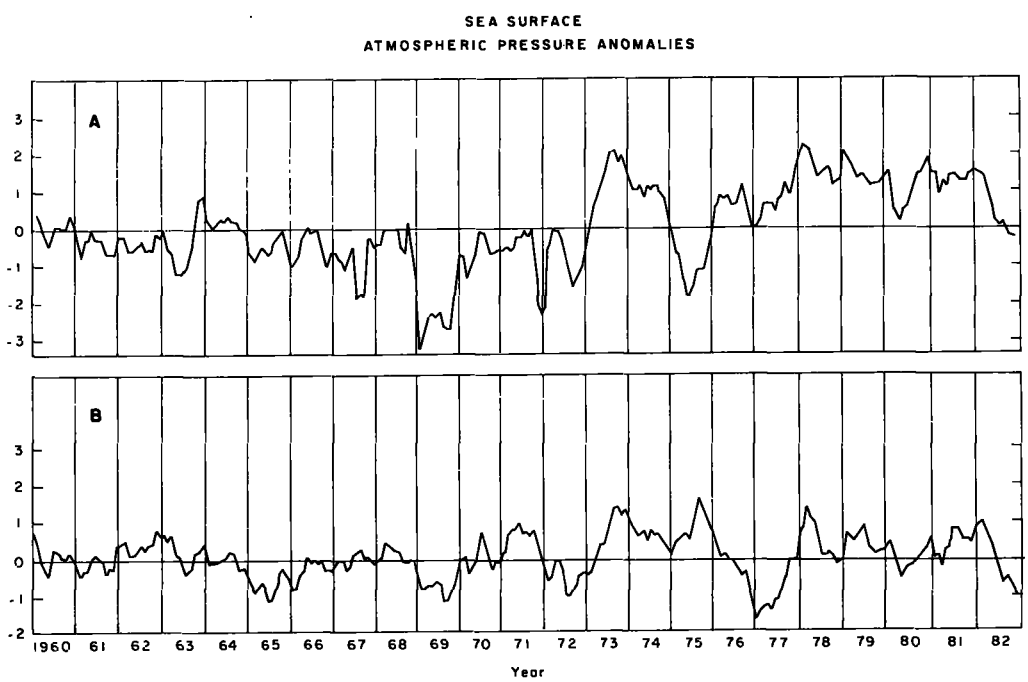

FIGURE 6.—Sea surface atmospheric pressure anomalies off of (A) Arica (18°S) and (B) Iquique (20°S), 1960–82. From Kelly and Blanco 1983.

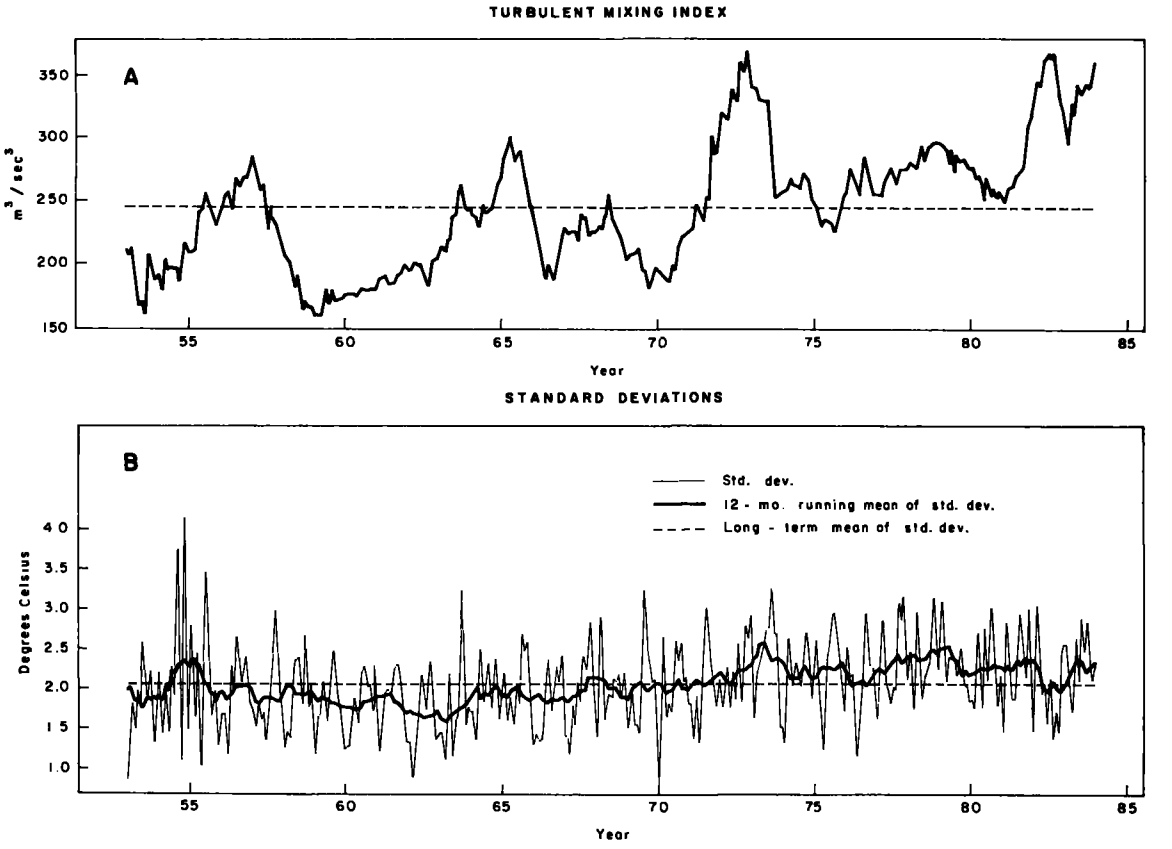

FIGURE 7.—(A) Surface layer turbulent mixing index values and (B) standard deviations and 12-mo running mean of standard deviations associated with mean monthly sea surface temperature values off of Peru (5°–15°S), 1953–84. Dotted lines represent long-term mean values of each index. From Bakun 1987.

conditions initiated during the warm 1968–69 period; these could possibly have persisted and intensified again during the 1976 and 1983 El Niño events.

It is also likely that the 1970 change in OL composition is related to onshore advection of northern or oceanic water masses and associated faunal assemblages, but this cannot be confirmed. All involved species are relatively abundant in coastal Peruvian and south eastern tropical Pacific waters (Ahlstrom 1971, 1972; de Castillo 1979; Santander and de Castillo 1979) and in more southern coastal Chilean waters (Table 2), but their wintertime relative abundances in these areas have not been documented. It is also possible that the changes in species composition are related to locally lowered zooplankton abundance (e.g., that the Group II species are relatively more successful than *Lampanyctus parvicauda* and *Triphoturus mexicanus* during periods of lowered secondary productivity levels). Alternatively, the observed change could be due to altered seasonal spawning activity which is not treated in the present study. However, whatever the cause, there is evidence for an environmental change in the study area, and this may be also implicated in changes occurring within the PL ichthyoplankton fraction.

Increased abundances of sardine and *Myctophum nitidulum* (Pair I species) during and after 1972 may be further evidence for a changed marine environment off of northern Chile. Additionally, the significant correlation between larval sardine abundance and temperature (Table 10) suggests that elevated temperatures may have been important for increased spawning activity and/or increased success of hatching and early larval survival. Given this observation one may speculate that the increased sardine catches after 1973 (Fig. 4) are related to increased frequency of warm-water events in the 1964–84 period relative to earlier years. Increased sardine

catches in 1973 resulted from apparently extremely good survival and recruitment of individuals spawned during the warm 1968–69 period (Serra[3]). Similarly, good survival of the large 1972 El Niño spawn could explain the huge catch increases in 1976 and later years (Fig. 4). However, mean biomass estimates of age groups contributing to the Chilean fisheries catch from 1974 to 1981 (Serra 1983) indicate increasing contributions after the 1967 year class with marked increases beginning with the 1970 year class; this suggests that factors other than temperature (e.g., environmental change starting in 1969–70) may also be responsible for increased larval survival and recruitment. A possible cause is increased nearshore influence of equatorial and subtropical waters (Santander and Flores 1983). Because the sardine abundance increase was initiated prior to the 1972 anchoveta decline off northern Chile (Fig. 4), it is difficult to implicate reduced anchoveta competition as the cause of the early sardine population growth in this area.

The grouping of anchoveta with three coastal species (Group I), and significant correlation of anchoveta and *Normanichthys crockeri* larval abundances are extremely interesting and imply that the spawning intensity and/or early stage survival of these four species are influenced in similar ways by interannual changes off northern Chile. Unfortunately, little is known about the natural histories or population abundances of the coastal species. Because of the group composition, it is logical to suspect that coastal processes are important factors influencing their larval abundance. The significant negative correlation of the group as a whole, and of two of the coastal species, with ranked temperature and salinity values (Table 10), suggests that coastal upwelling and/or increased coastal influence by subantarctic waters, and theoretically enhanced food supplies, are important factors.

Given the present data set and information from recent publications, a case can be made for a low-frequency environmental change influencing the abundances of anchoveta and sardine larvae as well as the larvae of coastal and mesopelagic species during the 1964–84 period. The Chilean OL composition suggests an environmental change (e.g., an atmospherically related oceanic circulation change) starting with the 1968–69 warm-water event. This coincided with apparent successful survival of sardine larvae and markedly increased recruitment by 1968 and later year classes despite varied warm water-cold water events between 1968 and 1973. Physiological anomalies of Peruvian anchoveta stocks in 1971 suggest that these fishes may have experienced environmental change at that time. Unusually low proportions (e.g., 40% vs. typically 90%) of potential spawning-sized fish were sexually mature during the 1971 spawning season and fat content of the 1971–72 catch was anomolously high, indicating unusually low transfer of body fat to gonadal products (Sharp 1980). Starting with the 1972 El Niño was 1) an obvious increased incidence of penetration of subtropical surface waters toward the Peruvian coast, 2) coincidental onshore and southward expansion of sardine spawning activity off both Peru and Chile, 3) southward expansion of Peruvian anchoveta spawning activity into new spawning areas between 14°S and 18°S (e.g., to northern Chile), and 4) a succession of years of poor anchoveta larval survival off Peru and Chile (Santander and Flores 1983; Serra 1983). Environmental conditions favorable for growth of sardine populations, as well as of mackerel and jack mackerel populations, off both Chile and Peru have persisted since the early to mid-1970's (Santander and Flores 1983; Serra 1983).

The lack of Chilean ichthyoplankton data from the 1974–82 period precludes evaluation of the constancy of altered species composition during that time. However, there are indications that change is once more occurring off northern Chile. Preliminary analysis of ichthyoplankton samples collected between Arica and Antofagasta during 4–14 August 1985 indicates a clear dominance by anchoveta larvae at a markedly higher mean abundance level than encountered in the 1964–83 samples; sardine and *Trachurus* larval abundances are comparable to those in the 1973 samples (Table 14). The other species have not yet been analyzed, but *Normanichthys crockeri* is

TABLE 14.—Mean abundance estimates and standard errors (numbers per 10 m^2) and percent frequency of occurrence (F) of PL taxa, OL and total larvae collected in 81 100–0 m WP_2 net samples off northern Chile (18°–24°S) during 4–24 August 1985.

Species	$\bar{X}$	(SE)	(F)
Engraulis ringens	5,535.3	(1,844.1)	(90.4)
Sardinops sagax	63.8	(24.9)	(26.6)
Trachurus murphyi	1.2	(0.9)	(2.1)
Other species	233.7	(28.4)	(92.5)
Total	5,834.0	(1,838.2)	

[3]Serra, R. Unpubl. manuscr. Subsecretaria de Pesca, Teatinos 120, Piso 11, Of. 44, Santiago, Chile.

once again noted to be among the abundant OL taxa. It will be of great interest to see the recruitment resulting from this 1985 anchoveta spawn. If the 1985 anchoveta year class is relatively successful during this period of continued large sardine stocks, it will lend support to the idea that the anchoveta-sardine population fluctuations have been primarily regulated by low-frequency hydrographic events. In a long-term context such events may not be unusual to the Humboldt Current area. Fish scales present in sediment records from coastal Peruvian waters indicate that sardine replacements of typically dominant anchoveta stocks have occurred at infrequent intervals over the past 11,000 years (De Vries and Pearcy 1982). In light of this, the ecological events of the past 20 years may be naturally occurring, physically mediated, but probably fisheries enhanced, fluctuations in this hydrographically complex region. Because of our limited time reference, we have not previously acknowledged such fluctuations as being "normal".

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ESTIMATION OF NATURAL MORTALITY IN FISH STOCKS: A REVIEW

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ABSTRACT

The instantaneous rate of natural mortality (M) is an important but poorly quantified parameter in most mathematical models of fish stock dynamics. This report reviews methods used commonly to estimate M for fish stocks, sensitivity of some common fishery models to values chosen for M, and evidence refuting the common assumption that a constant value can be an adequate approximation of M within single stocks.

With the exception of simple surplus production models (e.g., Schaefer 1954; Pella and Tomlinson 1969) all mathematical models of fish stock dynamics include as a parameter the instantaneous rate of natural mortality (M). The models do not require explicitly any particular form for M; it can be constant or can vary in any imaginable form. But because natural mortality has proved extremely difficult to measure directly, M is assumed almost universally to be some constant specific to whatever stock is being modeled. This is particularly true for analyses of commercial fish stocks, which often require estimates of M only for the postrecruit ages. Decreases in natural mortality with increasing age during egg and postlarval stages are so dramatic compared to apparent changes during postrecruitment ages (e.g., Cushing 1975) or compared to differences between different sexes, collection sites, seasons, years, cohorts, or stocks within species, that variations in M during these later (postrecruitment) ages are often assumed negligible.

Whether this assumption is in fact acceptable is the subject of this report. The answer is no, it is probably not acceptable in most cases. That answer follows from the information presented in Sections II through V, with the following conclusions:

Section II: Current methods for estimating natural mortality: a review of methods used currently to estimate M in fish populations. All of these methods have strong limitations or disadvantages.

Section III: Sensitivity of fishery models to choices for M: a review of the sensitivity of some standard fishery models to different choices for input value(s) of M. Existing studies show that the models are sensitive and that sensitivity is affected not only by the values chosen for M, but also by interactions between M and the values chosen for other parameters in the models.

Section IV: Evidence for nonconstant M; factors influencing death rate: a review of factors assumed or shown to affect M in fish stocks. Available information implies that many such factors exist, acting alone or in concert.

Section V: Evidence for nonconstant M; variability within and between groups: a review of existing quantitative evidence for the extent of variability in M between but especially *within* stocks. Because almost all fishery models focus on single stocks, variability within stocks (as opposed to between stocks) is the most important question. Some studies show strong differences between mortality rates of various groups of fish; some do not. Those which do not have tended to assume there would be none, and have often used catch curve regression analysis to derive a single estimate from data combined over many groups (usually years) of data. The few studies from which it is possible to determine ranges of estimates show differences of at least 50 to 100% between minimum and maximum estimates for single groups (e.g., stocks) of fish.

The report's major conlcusions are that natural mortality is far from constant for many fish stocks, and that this variability is extensive enough that it should not be ignored. Analyses of

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fish stock dynamics need much more rigorous estimates of **within-stock** variability (both trends and variance) in M for exploited fish stocks.

II. CURRENT METHODS FOR ESTIMATING NATURAL MORTALITY

Three methods are used currently or have been proposed to estimate M in fish populations: 1) analysis of catch data, usually from commercial fisheries but also from sampling programs specifically conducted for stock assessment (this includes mark-recapture studies), 2) correlations of M with other life history parameters, and 3) estimation of deaths due to predation. I describe below each method in turn, listing both advantages and disadvantages of each.

Catch-Analysis Methods

Methods for deriving estimates of natural mortality from catch data are based on measuring decreases in abundance, either relative or absolute, in groups of fish during two or more successive periods of time. Groups may be distinguished on the basis of any identifiable characteristic, e.g., size (length or weight), age, sex, location and time of capture, or some identifiable tag or mark.

The most common grouping is by age, for two reasons. First, age has been considered historically the most important factor potentially affecting estimates of mortality rate and subsequent results from the most commonly used fishery models (e.g., Heincke 1913; Baranov 1918). This is probably because the methods were developed for temperate water fisheries which tend to have obvious annual reproductive cycles, so that individual year classes are often relatively easy to distinguish. Second, the earliest method of estimating M (catch curve analysis, discussed below) depends on determining the rate during successive ages.

Regardless of the grouping criterion, methods for estimating M use generally one of two types of data. The first type is simply subsamples of unmarked catch. These subsamples contain fish selected randomly and classified into groups on the basis of size (length or weight). The second type is mark-recaptures, in which previously marked individual fish can be identified and classified after recapture into groups on the basis of this positive identification. Estimates of mortality are usually derived from samples of unmarked fish by analysis of resulting "catch curves" (Ricker 1975). Because it has been used so frequently, catch curve analysis is discussed below in some detail.

With marking it is possible to follow the history of individual fish, so many different types of estimation procedures exist for deriving estimates of mortality from mark-recapture data (e.g., Ricker 1975; Jones 1979; Brownie et al. 1985). Because so many variations are possible, marking experiments are discussed only generally, stressing the basic advantages and disadvantages of marking data relative to data from unmarked samples, in deriving estimates of mortality from these data.

Size-frequency distributions from unmarked subsamples of catch (the first type of data) are converted usually to age-frequency distributions, on the basis of previously determined relationships between age and length or age and weight. Subsequent analyses concentrate on analyzing this resulting curve of age-composition (e.g., Ricker 1975). Abundance usually decreases exponentially with size (or age) in this type of sample. Converting the abundances to their logarithmic values often results in a relatively linear decrease during most exploited ages (or sizes), after some initial increase in vulnerability. Graphs of these logged-frequency distributions are usually called "catch curves", and their analysis, "catch curve analysis". "Catch curve analysis" generally consists of determining the best-fit straight line through the decreasing portion of the logged-frequency distribution, because if the decrease in abundance is truly exponential, the slope of this line through the log-transformed data is the instantaneous rate of decrease in abundance (e.g., Ricker 1975).

There are two basic types of catch curves, distinguished on the basis of when the data were collected and how many groups are represented in the curves. The first, horizontal catch curves, includes data from several groups (e.g., size or age classes) collected at a single point in time (or combined from two or more points in time). Thus, horizontal catch curves reflect "ancient history". The individuals contributing to the frequency distribution were not originally all members of the same group. To use this type of catch curve, one must assume that for each successive age, risk of mortality has been historically the same for all individuals achieving that age. If this has not been the case, the catch curves may show various types of curvature in the descending leg, but absence of curvature is no guarantee that the rates have in fact been constant.

Thus, horizontal curves are subject to the extremely restrictive assumption that the groups from which the data were collected must be in steady state relative to each other, i.e., their relative abundances must be constant through time. If this is true, then a graph of data collected at a single point in time, which may include, for example, individuals from 5 consecutive year classes displayed as frequencies at 5 consecutive ages, will look the same as the 5 graphs of data that will result from collecting samples during 5 consecutive years (ages) from each of the 5 year classes. If these conditions are not met, simple linear fitting to determine a single estimate for mortality will be inappropriate.

The second type of catch curve, longitudinal, includes data collected from a single identifiable group over a protracted period of time. Most often, this will be a single cohort of fish such as single year class, sampled during successive years. Longitudinal curves are not subject to the assumption of steady state, but do share with horizontal catch curves several other severe disadvantages. These include 1) groups must be adequately identifiable; 2) groups must be closed to migration, so that changes in abundance are due only to fishing or natural mortality, or if migration does occur, it must occur in proportion to the age distributions in the local groups; 3) samples must represent adequately the true composition of the groups in nature; 4) rate(s) of mortality must be relatively constant between groups over time, so that the log-transformed frequency distributions are truly linear (e.g., Jensen 1984); 5) compensatory relationships between stock levels and natural mortality, or fishing mortality and natural mortality, must not be present.

Methods for estimating M, which assume to greater or lesser degrees that the conditions listed above are met, have been described repeatedly. The methods tend to fall into two categories. Methods in the first category estimate M from catch records of unexploited or lightly exploited groups of fish. In these groups, F equals or approximates zero. Therefore, the observed rate of decrease (Z) equals or approximates M, because Z equals the sum of F and M (e.g., Heincke 1913; Baranov 1918; Ricker 1947; Beverton and Holt 1957; Robson and Chapman 1961; Pauly 1982; Munro 1982; and among others).

Methods in the second category estimate M by determining Z at various levels of fishing effort, then using the observed relationship between Z and effort to predict, via regression analysis or manipulation of various ratios, the value of Z at zero effort (e.g., Silliman 1943; Beverton and Holt 1957; Paloheimo 1961; Lander 1962; Chapman and Murphy 1965; Paulik and Robson 1969; Gulland 1983; Butler and MacDonald 1979; Fournier and Archibald 1982; Caddy 1984; and others).

These methods are most appropriate for analyzing catches of unmarked fish. Accurate results depend strongly on accurate measures of catch per unit effort (CPUE) and constant catchability (q) because if these conditions (in addition to those listed above) are not met, observed relationships between abundances in different sample groups may not reflect true differences between groups in situ.

Marked fish present fewer problems. Advantages include 1) concentration on measuring relative rather than absolute differences between abundances of different groups, 2) immigration need not be considered, as entire original groups are known to carry marks, and 3) with sufficiently large samples, it becomes possible to test for differences in mortality rate between different groups (e.g., between ages, between sexes, or between sampling sites), rather than having to assume that such effects are negligible.

Reviews and descriptions of various mark-recapture methods appear in papers by Seber (1973), Ricker (1975), Jones (1979), and Brownie et al. (1985). Some of the newer types of marking analyses can solve many of the most vexing problems associated with traditional catch curve analysis (e.g., Reed and Davies 1980; Hochbaum and Walters 1984; Burnham and Andersen 1984; Burnham et al. 1984; Brownie et al. 1985).

Several disadvantages unique to marking operations counteract these advantages, however, even with the newer methods. These disadvantages include various types of mark-induced effects on mortality rates, behavior, and vulnerability to capture, as well as mark loss, unrepresentative mixing of marked fish with their original groups prior to recapture (e.g., Ricker 1975), and especially in commercial fisheries, underreporting or incorrect reporting of recaptures.

Both analysis of catch curves from unmarked fish and analysis of mark-recapture data have the advantage of requiring only catch (and usually effort) data, and these data can generally be collected by sampling catches from commercial fisheries. However, in addition to problems specific to each method, they have in common one or more other major disadvantages: 1) inability to distin-

guish between losses (or gains) from migration or recruitment versus losses due to fishing or natural causes, 2) imprecision in the estimates of M obtained (e.g., Beverton and Holt 1957; Taylor 1958; Bishop 1959; Paloheimo and Dickie 1966; Ricker 1975, 1977; Doubleday 1976; Pauly 1980; Larkin and Gazey 1982; Paloheimo 1980, 1982; Myers and Doyle 1983; Roff 1984), 3) sensitivity to size-specific mortality affecting the estimated age-structure of the group (Ricker 1969), 4) errors in estimates of age, such that abundances-at-age derived from age-length conversions are unrepresentative, 5) where analyses are conducted on data combined over two or more cohorts, the unlikely condition that mortality rates were in fact similar for all cohorts, and 6) problems inherent in the analyses themselves (e.g., Barlow 1984). Disadvantages 1, 4, and 5 may not apply to marked fish. Disadvantage 5 does not apply to single cohorts. But collections from marked groups and single cohorts are still vulnerable to the other problems.

Further, although in principle it would be possible to estimate M for different ages, times, or places, most commonly in practice a single, fishery-wide constant M is estimated by pooling data from throughout the fishery. By implication, the analyst is assuming that the exploited stock was more or less in steady-state over all times and areas of catch so that M was relatively constant while that data set was collected and while (historically) the observed age-distributions were being created. In fact, substantial evidence exists that M is not constant, either within a single stock over time (age) or between stocks of a given species in different areas (Sections IV and V).

A final disadvantage is that catch-curve analyses are fundamentally unmechanistic, generated simply by charting changes in abundance. Catch-curve analyses cannot predict the effect of changes in factors that control M; thus there is little hope of predicting M in the future should conditions change.

Life History Methods

A second approach to estimating the instantaneous rate of natural mortality in fish stocks is based on the observation that M often correlates strongly with life history parameters, such as growth rate, age at sexual maturity, costs of reproduction, and maximum age (Table 1).

Typically in such studies, analytical formulas are derived from theoretical relationships between the various parameters (e.g., Beverton 1964), or empirical formulas are derived from regression of M against one or more of the parameters (e.g., Hoenig 1983). These models have two significant advantages: 1) they require minimal amounts of data, and 2) they are useful in demonstrating broad trends across species and in developing ecological theory. But because they produce only a single and often very imprecise estimate of M for any given group of fish, they are not particularly effective for generating precise estimates of natural mortality or for determining the existence or extent of trends and variability in M for given stocks. They will also be no better than the methods used to estimate the values of M used in the regressions.

TABLE 1.—Studies relating instantaneous rate of natural mortality to life history traits in fish.

Traits	Species	Source
[1]T_{max}, [2]k, [3]L_{inf}, metabolic rate, reproduction	Various	Beverton and Holt 1959
T_{max}, k, L_{inf}, [4]L_{asm}, fishing	clupeids, engraulids	Beverton 1963
[5]W_{inf}	general	Ursin 1967
T_{max}, [6]$T_{max.biomass}$, k,	general	Alverson and Carney 1975
growth rate	young fish	Ware 1975
L_{asm}, gonad size, condition factor	gadoids	Jones and Johnston 1977
T_{max}	general	Blinov 1977
gonad/body weight index,		
[7]ASM, T_{max}, L_{inf}	general	Gunderson 1980
W_{inf}, L_{inf}, k, water temperature	175 stocks	Pauly 1980
energy cost of reproduction	general	Myers and Doyle 1983
T_{max}	various	Hoenig 1983
weight	various	Peterson and Wroblewski 1983
k, L_{inf}, L_{asm}	various	Roff 1986

[1]Maximum age.
[2]Von Bertalanffy growth parameter.
[3]Maximum length.
[4]Length at age of sexual maturity.
[5]Maximum weight.
[6]Age at occurrence of cohort's max biomass.
[7]Age of sexual maturity.

Predation Methods

A third class of estimators extends single species cohort analysis to a multispecies assemblage incorporating the major predators and alternative prey of the stock in question. Single species cohort analysis is used to estimate population abundances and annual values for the instantaneous rate of fishing mortality (F) for single groups, usually year classes, of fish (e.g., Pope 1972; Ricker 1975; Gulland 1983). The multispecies extension simply combines cohort analyses for several species (e.g., Anderson and Ursin 1977). The methods all generate estimates of M as the sum of some constant rate of nonpredatory, nonfishing mortality plus the total estimated flux of prey (stock) to each of the major predators. This feeding flux to predators is estimated by first using cohort analyses to reconstruct population sizes of the various groups of predator and prey, then combining these population sizes with observed growth rates for the predators and with estimated preferences for various prey. Thus it becomes possible to estimate the predatory component of M.

Versions of the method have been described by Anderson and Ursin (1977), Majkowski (1981), and Pope and Knights (1982). Applications in a marine system (North Sea) have been described by Anderson and Ursin (1977), in an ecosystem context, by Laevastu et al. (1982) and in lake systems by Forney (1977) and Stein et al. (1981).

The predation method has been developed primarily from analyses of marine systems, especially the North Sea, and much of the literature exists only as "mimeos" or notes associated with ICES (International Council for the Exploration of the Seas) activities. The most readily available discussion of this approach appeared in Mercer (1982), which includes a critical review and discussion by Ursin (1982) of the various methods. Several other discussions appear in Pauly and Murphy's (1982) volume of collected papers from a symposium on theory and management of tropical fisheries. Most of these papers specifically address tropical multispecies systems, but the concepts are broadly applicable. References to other, often less accessible, works can be found in these two general references.

The predation method is elegant in concept but often difficult to apply. Studies by Forney (1977) and Stein (1981) had the distinct advantages of limited species numbers in a small system, and direct quantification of stomach contents. Yet even in lake systems, the sampling problems of estimating Z, population abundances, and so forth, remain often as intractable as in large marine systems. The two greatest problems are 1) the difficulty in defining vulnerability and preference functions for the various prey stocks (e.g., Ursin 1982) and 2) the need to include cohort analyses of all the major interacting species, some or many of which may not be available commercially (and for which therefore data will be scarce).

Despite these problems the approach can certainly generate, for stocks that suffer heavy predatory mortality from other fished stocks, more realistic estimates of M than approaches that simply generate a globally fixed and invariant M. More importantly (and in contrast to the age-frequency or life history methods) the predation method has the advantage of being mechanistic. Predation-related causes and consequences of age, size, site, stock, geographic, or time trends in M can be investigated via perturbation and sensitivity analysis in computer simulation studies or, alternatively, investigated through analysis of existing catch data. It becomes possible (not necessarily feasible) to investigate the implications of varying age or abundance structures of interacting fishery resources.

Thus the predation approach has considerable conceptual appeal for fairly simple systems in which 1) predation is the major force controlling prey abundance, 2) predators have few alternative prey, 3) the possibility can be ignored that predators prefer moribund prey which were about to die anyway, and 4) all major species of predator and prey are sought commercially so that data on abundances and feeding preferences are or can be made available.

Unfortunately, the number of systems satisfying these requirements appears to be fairly small, and of course where predation is a relatively small fraction of M, the multispecies predation method will be particularly ineffective.

III. SENSITIVITY OF FISHERY MODELS TO CHOICES FOR M

Although catch-analysis, life history, and predation methods all exist currently for estimating M in fish stocks, in practice the only method used extensively is the first—direct estimation of M from analysis of catch structure. Thus the discussion below of model sensitivity to M is based on this type of estimate. The conclusions reached are

not specific to this one method. Model sensitivity to a given derived value of M will be the same, regardless of the method used to derive the value.

General Patterns

Sensitivity analyses of M in fishery models have evolved through two phases. Earlier studies noted the influence of M on estimates of maximum yield (Y_{max}) or maximum yield per recruit ($(Y/R)_{max}$), and on F_{max} (the fishing pressure required to produce maximum yield) in Beverton-Holt yield models (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Parks 1977; Bartoo and Coan 1979; Bulgakova and Efimov 1982). More recently, as cohort analyses have become more popular, more attention has been directed toward assessing the influence of M on age-specific estimates of stock sizes (N_i) and fishing mortalities (F_i) produced by these models (Murphy 1965; Pope 1971; Ricker 1971; Agger et al. 1973; Doubleday 1976; Ulltang 1977; Doubleday and Beacham 1982; Pope and Shepard 1982; Sims 1982a, 1982b, 1984). A few other studies have investigated the effect of M on estimates of maximum sustainable yield (MSY) or total biomass (Francis 1976; Deriso 1982; Beddington and Cooke 1983; Tyler et al. 1985).

Most of these studies have used a single, invariant value for M. Model sensitivity is then assessed by comparing model results using some "best" estimate of M, to results using one (or rarely, more) pair(s) of M values some arbitrary percentage above and below the best estimate. Only a few studies exist of the effects of nonconstant M, where M varies in different groups of fish **within** a given stock. These include Beverton and Holt's (1957) example of density-dependent M in plaice, and several investigations of age-specific M (Parks 1977; Ulltang 1977; Bartoo and Coan 1979; Sandland 1982; Bulgakova and Efimov 1982; Caddy 1984; Tyler et al. 1985).

No study to date has specifically addressed the problems of estimating values of M for a full fishery analysis, leading from cohort analyses (using M to estimate F_i, N_i, and recruitment R) to estimates of yield or yield-per-recruit using the same M(s) and R subsequently in the Beverton-Holt formulas. Also, no study to date has addressed the possibility and consequences of differing patterns of variability in M, although it has been suggested in one case (Ulltang 1977) that random variations will be unimportant if the rate is constant (on average) over the fished ages.

In general, the earlier analyses with yield models assuming a constant M show that *higher* estimates of M lead to 1) **lower** estimates of Y_{max} or $(Y/R)_{max}$ (because fewer survive to be caught), 2) *higher* estimates of F_{max} (you must fish a bit harder to catch a given amount of those left), and 3) **lower** estimates of age at first capture (t_c; because it pays to catch them before they die, rather than waiting for them to grow bigger but less abundant).

Including density-dependence tends to exaggerate these trends, at least for plaice in the North Sea (Beverton and Holt 1957). Including age-structured M in yield models also affects the estimates, but not necessarily in a straightforward manner. As described below in the section on numeric results, change in model output for a given change in M depends not just on the values chosen for M, but also on those chosen for the other parameters. M is not an independent parameter in these models.

Analyses with cohort or virtual population models which assume a constant value for M show that in general the effect of increasing M is to increase estimates of N_i (because the higher M is, the more fish died in addition to those being caught) and to decrease estimates of F_i. The data show only Z, which is the sum of M and F_i. Assuming Z has been constant, a decrease in F_i requires an increase in M. If Z has been variable, the lower F_i may be explained on the basis of higher N_i, a smaller proportion of which (F_i) would account for the observed catch.

The actual effect, particularly on estimates of N_i, is not necessarily that simple. As with yield models, a given change in M does not always produce the same change in model output. The result depends also on values chosen for other parameters; M is not an independent parameter.

In cohort analysis the results (estimates of N_i and F_i) are particularly sensitive to the relative sizes of F and M (i.e., to the exploitation ratio $E = F/(F + M)$). The effect of assuming an incorrect value (or series of values) of M tends to build up as the analysis proceeds backward in time. This is because with every time step backward the catch (C) is inflated by the factor M in order to estimate at that time the size of the entire stock, not just the size of the catch. That is

$$N_i = N_{i+1} + C_i(F_i + M)/F_i \quad (1)$$

where F_i satisfies the catch equation

$$C_i = N_{i+1}\,(F_i/F_i + M)\,(e^{(F_i+M)\,t} - 1) \qquad (2)$$

If M is large relative to F (i.e., the exploitation ratio is low), then errors in N_i can increase progressively and become quite large at the younger ages (e.g., Agger et al. 1973; Murphy 1965; Ulltang 1977; Sims 1982a, 1982b, 1984).

Numeric Results

Although general responses of various models can be determined simply by inspection of the analytic models themselves, the quantitative change to expect in the result (output) for a quantified *change* in M (input) is not always immediately obvious. This is because M tends to occur more than once in various formulas. For example, M appears in both the numerator and denominator in the solution to the Beverton-Holt yield equation (Ricker 1975).

$$\begin{aligned} Y = FN_0e^{(-Mr)}W_\infty(1/(M + F) \\ - 3e^{(-kr)}/(M + F + k) \\ + 3e^{(-2kr)}/(M + F + 2k) \\ - e^{(-3kr)}/(M + F + 3k)). \end{aligned} \qquad (3)$$

So, rather than derive analytical expressions (e.g., Sims 1984), I resort below to a simpler approach. Sensitivity of fishery models to changes of given magnitude in M is assessed by comparing percent change reported in model response (output) to percent change in M (input). In cases for vector (age or density-dependent) M, I have merely described the shape of the M-vector. For these different vectors, I report the percent change in the result due to switching from a vector of one shape to a vector of another shape.

Yield Models

At least four studies (Beverton and Holt 1957; Hennemuth 1961; Francis 1974; Bartoo and Coan 1979) have shown that errors in estimates of M propagate into roughly equal errors in estimates of $(Y/R)_{max}$, but with sign reversed (Table 2). For example, a 10% overestimate in M will lead to approximately 10% underestimate of $(Y/R)_{max}$. An equally important result is that the actual magnitude of the effect induced depends strongly not just on the error in M, but on the values chosen for the other parameters in the model.

In another study, Beddington and Cooke (1983) used the Beverton-Hol formulation to investigate the influence of M (constant; 0.1 to 0.8 year^{-1}), t_c (0 to 4 years), and K (the von Bertalanffy growth parameter; 0.1 to 0.5 year^{-1}) on MSY (maximum sustainable yield), expressing the result as "MSY as a % of B_0," where B_0 is the initial or recruited biomass. Higher percentages indicate that more of the original biomass is being taken at MSY. Increasing M by a factor of 8 (0.1 to 0.8 year^{-1}) increased MSY/B_0 by a factor of about 4 to 8, depending on the particular values of t_c and K. Again, errors in M produced roughly the same relative error in the result; and again the actual effect of any given change in M de-

TABLE 2.—Sensitivity of estimated maximum yield per recruit ($(Y/R)_{max}$) to changes in instantaneous rate of natural mortality (M) and other input conditions. Sensitivity of $(Y/R)_{max}$ and of changes in M are expressed as percentage difference from nominal responses at nominal (best-guess) M. Symbols are: t_c = age-at-first-capture, F = instantaneous rate of fishing mortality, M = nominal value for M. Frances (1974) used an age-structured simulation model. All other citations used standard yield-per-recruit analyses.

Input conditions	% change in M	% change in $(Y/R)_{max}$	Species	Source
t_c = constant (3.72) F = variable M = 0.10	+50 −50	−20 +30	plaice	Beverton and Holt 1957
t_c = variable F = constant (0.73) M = 0.10	+50 −50	−60 +50	plaice	Beverton and Holt 1957
F = constant (0.95) M = 0.8	+20 −20	−21 +32	yellowfin tuna	Hennemuth 1961
M = 0.8	+10 −10	−14 +16	yellowfin tuna	Francis 1974
M = 0.60	+25	−20	yellowfin tuna	Bartoo and Coan 1979

pended on the values chosen for the other parameters.

Pope and Garrod (1973) present another example of sensitivity in MSY to values chosen for M. They describe briefly the consequences of using an incorrect constant for M of cod stocks when estimating the F required to generate MSY (F_{MSY}). Underestimating M by 50% (assumed $M = 0.1$ year^{-1}; true $M = 0.2$ year^{-1}) leads to a choice of F_{MSY} that is 67% too high. Overestimating M by 50% (assumed $M = 0.3$ year^{-1}, true $M = 0.2$ year^{-1}) underestimated F_{MSY} by 50%.

The simulations described above tested the effects of choosing alternative constant values for M. Choosing a vector alternative can also have significant effects; again, the magnitude of the effect depends on the values chosen for other parameters. Beverton and Holt (1957) showed that incorporating density-dependence in M for plaice decreased $(Y/R)_{max}$ by 12%, when holding t_c constant at 3.72 years and letting F vary. Conversely, holding F constant and letting t_c vary decreased $(Y/R)_{max}$ by about 37%.

Age-dependent values for M were compared with age-constant values by Bartoo and Coan (1979), Bulgakova and Efimov (1982), and Tyler et al. (1985). In their analysis of Atlantic yellowfin tuna stocks, Bartoo and Coan found that replacing an assumed constant M of 0.8 year^{-1} with an age-structured M increasing from 0.1 year^{-1} at age 0 to 1.2 year^{-1} at age 7, increased $(Y/R)_{max}$ by 17% (from 6 to 7 kg).

Estimating total yield (Y_t) rather than (Y/R) and estimating R as a function of constant versus age-specific M in analysis of catch curves for relatively unexploited stocks of Pacific ocean perch and Oregon hake, Bulgakova and Efimov (1982) found that replacing a constant (age-averaged) M with age-variable M tended to increase estimated Y_t when fish recruited fairly late to the fishery, but decreased Y_t if the fish recruited early. This is because of the interaction between the values assumed for M (constant or age-variable) and the value calculated for R from each type of mortality curve.

Starting with a given value for recruitment at age 6 years (from Efimov 1976), they calculated R twice for ages 4 and 8 years—once with age-averaged M and once with age-specific M. Because in this set of data the age-averaged M was generally higher than the age-specific M at the tested ages of recruitment (ages 4, 6, or 8 years), back-calculations with age-averaged (i.e., constant) M predicted fewer recruits than back-calculations with age-specific M. With fewer recruits and generally higher M, potential yield at later ages obviously must drop. Differences in predicted potential yield ranged from about −30% at t_4 (age-specific estimate lower than age-averaged estimate, when fish were assumed to recruit to the fishery at age 4 years) to +15% at t_6 (age-specific estimate higher) and to +60% at t_8.

Tyler et al. (1985) tested (among other things) the effects of ignoring "true" age-structure in M and using instead a constant value in estimating stock biomass using Deriso's (1980) delay-difference model. They did the tests on catch data generated by Walter's (1969) age-structured simulation model of cod, using three different (input) age structures for M in Walter's model. After generating "catch data" from Walter's model, they analyzed the simulated data set using Deriso's model with constant M (= 0.5 year^{-1}). The age structures tested were 1) mortality increasing and then decreasing with age (Walter's original mortality vector spanning ages 3 to 12 years; age-averaged $M = 0.55$ year^{-1}, range = 0.33 to 0.70 year^{-1}), 2) mortality increasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.3 to 0.7 year^{-1}) and 3) mortality decreasing with age (ages 7 to 12 years; average $M = 0.5$ year^{-1}, range 0.7 to 0.3 year^{-1}). In all three cases Deriso's model with constant M misestimated the "true" biomass generated by Walter's model (with age-structured values for M). The differences were relatively small, however: −13% for the increasing and then decreasing series, +19% for the decreasing series, and +4% for the increasing series. These differences were due to the differences in M, and not the differences in model structure; generating and analyzing biomass with the same constant M in both models led to a discrepancy of only 0.5%.

By analogy to life history patterns in other adult animals, M (after recruitment into most fished stocks) is more likely to increase with age than to cycle or decrease. By implication, the simulation results from the increasing series are probably most realistic. If so, the effects of ignoring age-structure in favor of using a constant M may be relatively small (5 to 20%), at least for the cod stock simulated in this study. But the results obviously depend again not just on correctly choosing the values for M, but on the values chosen for the other parameters. In this case, Tyler et al.'s (1985) results imply that age-structure in M can be relatively unimportant, at least when the

assumed constant is evenly bracketed by the "true" age-structure in M.

Further simulations by Tyler et al. (1985) using a wide range of constant values for M (0.4 to 1.4 year^{-1}) and the growth rate parameter rho (mean Ford growth coefficient for the fishable stock; 0.46 to 1.6) showed that incorrect guesses of M (and rho) could produce errors up to 1,000% in estimated biomass. More realistic ranges for the two parameters (0.4 to 0.8 year^{-1} for M, 0.6 to 1.2 for rho), extending about 50% above and below the "true" values for these parameters, induced much lower error in biomass estimates (about the same order of magnitude, 50 to 100% below and above the "true" biomass). As before, changes (errors) of a given amount in M (expressed as fraction or percentage of the original value) appear to produce about the same amount of change (expressed as percent of original value) in simple estimates of yield, depending on the conditions of other parameters in the model.

Chatwin (1958) compared estimates of Y_{max} from lingcod populations. Rather than compare constant and age-variable values for M, he assumed several different values for an average (constant) M in adults, but assumed that M increased from the assumed average for adults to higher values in both juveniles and senescent fish. He reports no quantitative results but states, as found above, that increasing the average M, for a given F, considerably decreased Y_{max}, that decreasing M increased Y_{max}, and that size at first capture changed relatively little with those changes in M.

These comparisons between age-structured versus constant M, or between different constants have demonstrated that effects on results can be large for some combinations of parameters yet small for others. Alternative choices drawn from apparently realistic parameter values lead to relatively small differences in estimates of M. Specific amounts of change depend strongly not only on the values chosen for M, but also on the value of M **relative** to values chosen for the other interacting parameters in the yield models. For most choices of parameter values, sensitivity of output is roughly equal to perturbation of input.

Cohort Analyses

Effects of interactions between changes in M and values chosen for other parameters is even more obvious in stock reconstruction analyses (e.g., cohort analysis and virtual population analysis (VPA)). These analyses are used to "reconstruct" estimates of stock abundance during previous years, based on catch data and assumptions about the value(s) of M during those previous years. Studies of sensitivity to M in Beverton-Holt types of yield or biomass assessments were usually empirical, based on analyses of catch data from specific fisheries. Studies of sensitivity to M in VPA and cohort analysis include both theoretical and empirical studies; i.e., simulations using totally contrived data sets (e.g., Agger et al. 1973), analyses of specific data sets (e.g., Pope 1971; Doubleday and Beacham 1982) and combinations of analytical evaluations and analysis of specific data sets (e.g., Doubleday 1976; Ulltang 1977; Sims 1982a, 1982b, 1984).

Simple analyses of sensitivity to M, in which M is varied but all else is held constant, include 1) Pope's (1972) analysis of Atlantic yellowfin tuna, in which he found that replacing constant M with age-structured M (higher Ms for older fish) produced lower estimates for fishing mortality (F_i) in the later ages, but had little effect on estimates for the younger ages, and 2) Doubleday and Beacham's (1982) statement that 10% error in constant M translated into 9 to 14% error in estimates of R (at age 3) for cod in the Gulf of St. Lawrence.

Somewhat more complicated analyses are presented by Ulltang (1977) and Sims (1982a, 1982b, 1984). Ulltang evaluated the effects on model predictions of F_i and N_i, of several types of variation in M. These included no variation (uniformly constant M), M constant within years but varying randomly between years, M varying with age, and M varying with season. Sims evaluated the effects of choosing various constants for M on estimates of N_i, and derived an analytical expression relating variance in M to expected variance in estimates of abundance.

In Ulltang's simulations, increasing (decreasing) a constant M by 50% (from 0.2) decreased (increased) F by about 20% ("true" F's ranging from 0.4 to 0.8). Creating a data set with M varying randomly from one year to the next, then analyzing those data with an assumed constant M, Ulltang (1977) found that the Z calculated from the constant-M model was on average the same as the "true" Z from the random-M model. He concluded that random fluctuations in M will cancel out during analysis and so can be ignored. Ulltang assessed the influence of age-dependent M compared with constant M by generating a catch curve with age-variable M (decreasing curvilin-

early from 0.3 at age 1 to 0.1 at age 10, average about 0.2) and F equal to 0.2, then analyzing the catch with F equal to 0.2 or 0.6, and M equal either to 0.1 or 0.2. Choice of M made little difference in estimates of stock size for the case of high F (0.6), because most of the deaths were due to (observed) fishing. When F was low (0.2), stock-size estimates were much more sensitive to incorrect choices for M, because most of the deaths were due in this case to M, which was unmeasured and therefore unobserved.

Ulltang (1977) simulated seasonal changes in M by concentrating all deaths in either the first or last quarter of a year. Estimated stock sizes (N_i) changed relatively little; with $F = 1.2$ and $M = 0.4$, N_i was a maximum of 10% higher if all deaths occurred first quarter, 10% lower if all occurred in the last quarter.

A serious problem with the conclusions reached by Ulltang (1977) is also common to all the other studies discussed above; they are based on relatively few combinations of values for the various parameters, and relatively few simulations. For example, the conclusion that random errors in M will tend to even out is intuitively attractive, provided the time scale of variation is short relative to the generation time of the fish. In fact random variation in M did even out in the two sets of simulations he conducted. But the examples he chose included only one set of ages (2 to 10 years), with relatively high values of F (0.5 to 0.8 year^{-1}) compared to the values tested for M (0.1, 0.3 year^{-1}). The gravity of consequences from choosing an incorrect M depends very heavily on the size of M **relative to** the size of F, i.e., on E. Had he chosen different values for his simulations, he might have reached very different conclusions. This is probably the basis for the discrepancy between Ulltang's conclusion that seasonal effects are minor, versus Sims' (1984) conclusion that seasonal effects can be quite large, if M is high.

Sims (1984) attempted to overcome this problem (trying to draw general conclusions from the results of simulations based on particular, or relatively few, sets of parameters) by analytically deriving formulas for relative error in stock-size estimates, and then testing the formulas with data from actual fisheries. He used this approach twice: once to assess the effects of seasonality (Sims 1982a) and once to consider in general the effects of different choices (errors) for constant M (Sims 1984). But his results (and equations for error) show clearly that error in estimated stock sizes depends on several parameters and that the effects of one can be strongly dependent on the values chosen for the others. Choosing a high M (0.6 year^{-1}) and concentrating catch during the first quarter of the year overestimated R by 20%; concentrating catch during the last quarter underestimated R by 23% (compared with the 10% error found by Ulltang).

Within the same analysis, reducing M by half (to 0.3 year^{-1}) reduced the error in R by half, but the same reduction of error in R was also achieved by leaving M high and reducing F. In assessing specifically the effects of error in M on error in R, Sims (1984) showed very different effects on estimates of R in heavily fished versus lightly fished cohorts of Atlantic bluefin tuna. Changing M by 50% led to changes in estimated R of 60 to 260% in the lightly fished cohort, but only to relatively smaller changes of 35 to 70% in the heavily fished cohort. Again, the magnitude of the error in model predictions depended not just on the magnitude of M, but on its relationship to the other parameters in the catch equation, particularly F.

Errors (expressed as percentage change in output for a given change in input) in model output in the simulations described above, all of which tried to use apparently realistic values for model parameters, rarely exceeded 50%, and were often less than the error introduced into values chosen for M. By implication, the effects of incorrectly guessing M may be relatively unimportant if M is relatively small (e.g., in this situation not more than about 0.5 year^{-1}) and relatively invariant, although the actual magnitude of effect due to any given percentage change in M depends on the values chosen for other parameters.

So, inaccurate estimates of M might be important or they might not. It all depends on the magnitude and variability of M within a **given stock** (or group). Although untested, it seems likely that estimates of M for groups in which M varies little and is relatively low, are more likely to be reasonably accurate than estimates of M from groups in which M is large and variable. The following section reviews evidence that M does in fact vary both within and between groups of fish, and the succeeding section reviews evidence for the magnitude of that variability in ostensibly similar groups.

IV. FACTORS INFLUENCING DEATH RATE

Despite the fact that in most fishery models, M is assumed to be constant for all exploited ages in

any given stock, abundant evidence exists to the contrary. Natural mortality has been shown to vary with age, density, disease, parasites, food supply, predator abundance, water temperature, fishing pressure, sex, and size. Evidence for relationships between these factors and M, and selected references for each, are presented below.

Changes in mortality rate with **age**, within single groups of fish, have been demonstrated and discussed more frequently than changes with any other factor. References include, among others, Baranov (1918, plaice), Sette (1943, Atlantic mackerel), Ricker (1945, 1947, lake fish; 1969, 1975, various species), Beverton and Holt (1959, many species of marine fish), Beverton (1963, engraulids and clupeids), Boiko (1964, sturgeon), Cushing (1975, plaice), Blinov (1977, fish in general), Bulgakova and Efimov (1982, Oregon hake and sea perch), Sandland (1982, fish in general), Smith (1985, clupeoids), Roff (1986, fish in general). Evidence for changes with senescence for fish in general has been discussed or documented by, among others, Woodhead (1979) and Craig (1984).

Although specific patterns vary with species (e.g., Woodhead 1979), in general M is extremely high during egg and larval stages (e.g., 2 to 10% per day in plaice and clupeoids (Cushing 1975; Smith 1985)), falls precipitously during the juvenile period, becomes **relatively** stable during intermediate adult ages and increases again with senescence. But even during these relatively stable mid-adult ages, changes in M with age can be substantial, particularly in short-lived fish (e.g., Ricker 1947, stunted versus "normal" whitefish).

Changes in natural mortality rate with **size** (rather than age) within single groups of fish (usually stocks), have been discussed by Baranov (1918, plaice), Ricker (1969, size-selective mortality in general), Ware (1975, larval fish), and Peterson and Wroblewski (1984, many species). Differences in natural mortality rate between populations of the same species in different environments, or even in different areas of a single environment (e.g., a single lake) are documented by Ricker (1947), Kennedy (1954), and Schupp (1978). Year-to-year differences in natural mortality rates of single stocks from a given area are shown by Pope and Knights (1982, plaice) and by Henderson et al. (1983, whitefish). Density-dependent changes in M are discussed by Beverton and Holt (1957), Cushing (1967), Tyler and Gallucci (1980), Backiel and LeCren (1978), Jones (1982), and others. Differences in M between sexes have been documented by Beverton and Holt (1957, plaice), Ricker (1947, rock bass), and others. Changes in natural mortality rate related to the cost of reproduction have been discussed by Jones and Johnston (1977), Roff (1984), and others.

Other factors that affect M either alone or in combination with other factors include disease and parasitism (reviewed by Lester 1984), starvation (Hewitt et al. 1985; Theilacker 1986: larval anchovy), physiological state (Smith 1985), and fishing pressure (Ursin 1982; Munro 1982). Additional examples are cited by Beverton and Holt (1957), Anderson and Ursin (1977), Sissenwine (1984), and Hunter (1984).

Most of the factors listed above (e.g., age, size, sex) are indirect influences on M. The most important factor directly affecting natural mortality rate is probably predation; this is implied by a large body of literature describing changes in prey community composition and abundance following changes in composition and abundance of predators (e.g., Carpenter et al. 1985).

Direct evidence that predators account for most natural mortality in fish stocks is difficult to gather (Section II). To quantify the fraction of M due to predation, one must know, not only relative changes in abundance, but absolute population density of all predators and prey together with consumption rates and prey preferences of all the predators. Although this is rarely possible, at least two studies from freshwater systems do present quantified estimates of predatory mortality in relation to available prey. Forney (1977) quantified predation mortality in a relatively simple, unmanipulated lake system where there were few species of predator and prey. Combining stomach-content estimates of prey consumed with trawl-sample estimates of predator and prey abundance, he concluded that 30 to 100% of yellow perch production was consumed by walleye, their principal predator. In a manipulated system, Stein et al. (1981) assessed predatory mortality of young tiger muskellunge after they were stocked in a small pond and lake. During the time of the study, a single predator (largemouth bass) accounted for 25 to 45% of losses to natural mortality.

In marine systems evidence for the relative importance of predation can be gleaned from comparing total natural mortality with estimated predatory mortality based on abundance of predators and feeding preferences. For example, multispecies cohort analyses reported by Pope and

Knights (1982) show predatory mortality as 80 to 90% of M for age-0 cod, whiting, and haddock in the North Sea (the fraction of M due to predatory mortality cannot be assessed accurately in the older ages because predators appropriate to these sizes were not included in the analysis). In another example, estimating M from energy flow models, Sissenwine (1984) demonstrated that predation in the Georges Bank ecosystem can account for all production by prey fish; nonpredatory mortality was negligible.

Thus a multitude of factors, acting alone or in concert, can be expected to produce variations in M between individuals within single groups of fish, as well as between groups. Differences can be expected between species, between stocks within species, and from place-to-place and time-to-time within given stocks. In the following section, I will review more completely existing evidence for, and the extent of, this expected variability in M.

V. VARIABILITY WITHIN AND BETWEEN GROUPS

As discussed above (Section III), simulation studies generally show that effects of choosing a particular value or set of values for M can range from insignificant to considerable, depending in part on the model used, in part on the values chosen for other parameters, and in part on the form chosen for the estimate(s) of M. Authors suggest that in the future, simulations should be conducted with a range of values for M, to bracket probable values (e.g., Beverton and Holt 1957; Tyler et al. 1985).

The problem with this advice is identifying the appropriate range and distribution of M for any given group of fish. Obviously, wide ranges for M will lead to great discrepancies between model predictions based on one end of the range or the other. It has been shown above, however, that model output can be relatively **insensitive** to small changes in M. This is particularly true if F is much larger than M (i.e., if the stock is highly exploited so that losses to fishing far exceed losses to natural mortality). The problem is determining whether, for a given stock in situ, changes in M are in fact large or small. Compensatory changes in M, in response to changes in F, will further confound the problem, because variations in M will then be a function of the value(s) of F, in addition to the suite of other factors that may be affecting estimates of M.

M does appear to vary considerably **between** groups of fish. Estimates of M compiled by Pauly (1980) (Fig. 1) for 175 stocks and species of fish worldwide differ greatly between groups, ranging from a minimum of about 0.1 $year^{-1}$ to several unusual values as high as 7.0 $year^{-1}$. Even within a group as ostensibly homogeneous as the tunas, the range of estimated mortality constants spans the majority of the common values (0.2 to 2.0 $year^{-1}$, Murphy and Sakagawa 1977).

Estimates of variability in M **within** groups of fish are much less common, but are actually more important than the obvious differences between groups with obviously different characteristics such as differing lifespans. Most fishery analyses are directed toward understanding or predicting dynamics of single stocks (single groups of fish). The most important considerations for natural mortality parameter values in these single-species analyses are whether and if so over what values M varies for the group of fish in question.

But measuring trends or variability in natural mortality rates **within** given groups (e.g., stocks) is difficult and, with the exception of trends with age, rarely attempted. This is primarily because the only extant methods for estimating M depend either directly or indirectly on analysis of catch data (Section II), and catch data are prone to many well known (but largely unsolved) problems.

Problems with analysis of catch data fall into two general categories: 1) problems with sampling procedure, such that fish are caught or counted out of proportion to their true abundance and 2) problems with fish appearing or disappearing from the "unit stock" due to causes other than birth or natural mortality (i.e., migration, fishing mortality, or tagging mortality), again resulting in catch data that do not represent the true structure of the stock. If sampling biases can be overcome, the problem reduces to partitioning total disappearance of fish into fractions owing to fishing, tag mortality, and migration. The first partition can be eliminated by studying unfished populations, the second by quantifying tag mortality, and the third by studying only closed or tagged populations.

Unfortunately, very few sampled populations satisfy completely even one of these criteria. Regardless, we still need at least some crude estimates of M in order to determine whether M truly varies enough to invalidate the standard assumption in fisheries models that M is effectively constant during exploited ages. The question here

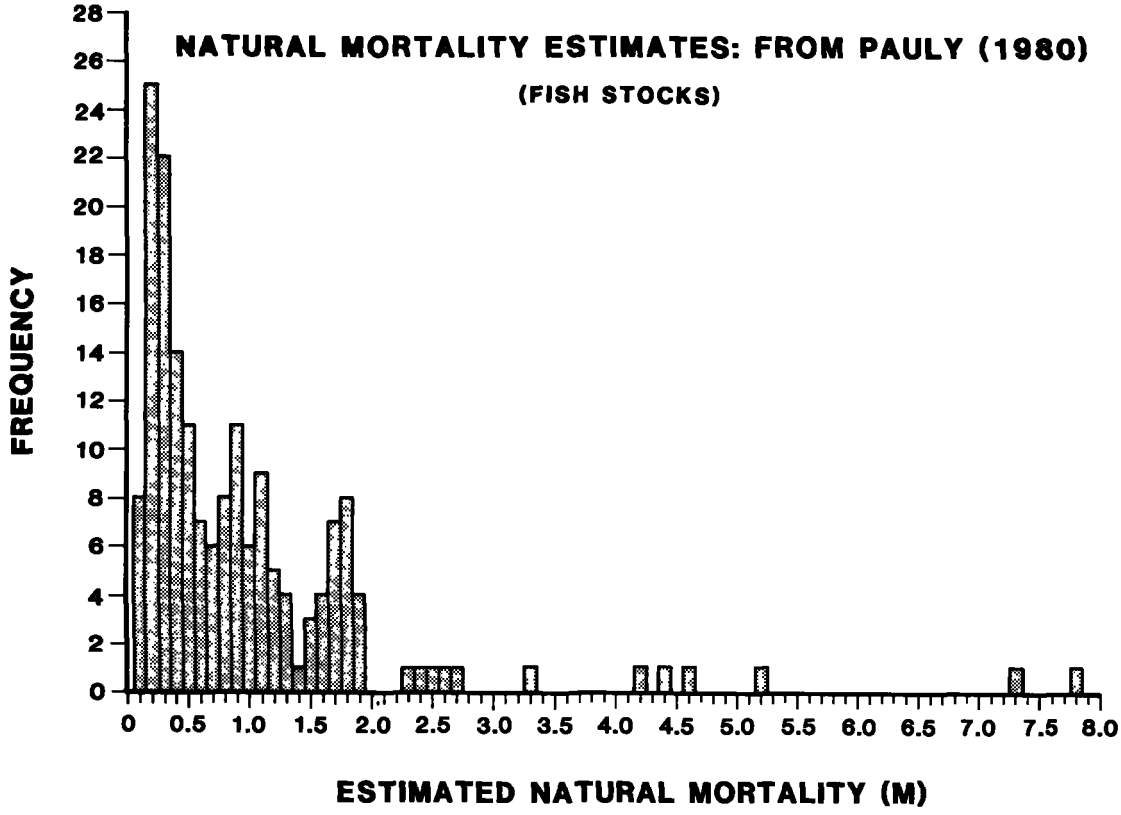

FIGURE 1.—Frequency of estimated instantaneous annual rates of natural mortality (M) in 175 different fish stocks, populations, or species. Estimates include both freshwater and marine species. Data from Pauly 1980.

concerns variability of M **within** groupings that would be used commonly to estimate M, such as stocks of single species, rather than general patterns across species. If M truly varies relatively little during these ages (so that the log of catch-at-age decreases linearly with age), if the age structure has been relatively constant historically (so that catch curves are actually linear, rather than curvilinear as seen in stocks with inconstant age structure, e.g., chapter 2, Ricker 1975), and if catch curves actually reflect relatively accurately this constancy and low variability, then most estimates of M derived from analysis of appropriately processed catch curves cannot help but be relatively close to the true rate. Model predictions, although in theory sensitive, would in practice be fairly robust to any particular value chosen from the true range of values for M.

Despite the potential problems with accuracy or precision of existing estimates from single groups of fish, I list in Table 3 most of the estimates available for unexploited populations, and some of the few existing estimates from exploited populations. My purpose is to identify the apparent range of variability in M within single stocks. The estimates are drawn from references cited by Pauly (1980) and other sources. Only references that reported multiple estimates for M are included, thus excluding most of the references reviewed. Because these estimates are derived from catch data, the stated ranges are "apparent", rather than demonstrably the "true" values.

Estimated rates of natural mortality are not particularly constant for either unexploited or exploited groups, and are only slightly less variable within stocks than they are within species. Although the range of rates within groups may appear relatively small compared to the total range of rates reported for all fish species (e.g., 0.36 to 0.56 for sauger from Lake Nipigon [Table 3] vs. approximately 0.1 to 3.0 for most species listed by Pauly 1980), the maximum and minimum rates reported for single groups differed by at least 50% in 20 of the 22 comparison listed in

Table 3. In at least one case maximum and minimum estimates differ by as much as a factor of 7 (i.e., young vs. old whitefish in Shakespeare Island Lake, Ricker 1947, Table 3).

The range of reported estimates of M for species (rather than single groups or stocks within a species as compared above) is even greater. Even the least variable estimates differed by a factor of 1.75 (75%, male vs. female plaice, Beverton 1964). In whitefish, the species for which the most estimates exist, maximum estimates are **20 times** greater than minimum estimates (Table 3).

TABLE 3.—Ranges in estimates of instantaneous rate of natural mortality in unexploited and exploited fish populations. M_{max}/M_{min} is expressed as the ratio between the maximum (M_{max}) and minimum (M_{min}) values reported for M for that species, Values in parentheses are total range of estimates and ratios for those species where multiple reports exist.

Species name	Common name	Body of water	Sex	Age (years)	M range	M_{max}/M_{min}	Source
I) Unexploited populations:							
Amboplites rupestris	rock bass	Nebish Lake	m	10–12	1.47–2.1	1.49	Ricker 1947
		Nebish Lake	f	10–14	1.1–1.6	1.45	Ricker 1947
		Nebish Lake	both	10–14	1.08–1.56	1.44	Ricker 1947
					(1.08–2.1)	(2.01)	
Stizostedion canadensis	sauger	Lake Nipigon		8–14	0.36–0.56	1.56	Ricker 1947
Coregonus clupeaformis	whitefish	Lake Opeongo		6–13	0.53		Ricker 1947
		Shakespeare Island Lake		11–27	0.08–0.60	7.51	Ricker 1947
		Great Slave Lake		17–22	0.71–0.99	1.39	Kennedy 1953
		Lake Nueltin		13–15	0.84		Kennedy 1963
		Lake McDonald		11–14	1.34		Kennedy 1963
				9–10	1.66		Kennedy 1963
					(0.08–1.66)	(20.75)	
Leucichthys sardinella		Ikroavik Lake		6–10	0.2–1.4	7.00	Wohlschlag 1954
Cristovomer namayacush		Great Slave Lake		1–26	0.31–1.61	5.19	[1]Kennedy 1954
		Great Slave Lake		15–23	0.49–0.92	1.88	[1]Kennedy 1954
		Great Slave Lake		15–23	0.52–0.75	1.44	[2]Kennedy 1954
					(0.31–1.61)	(5.19)	
Perca fluviatilus	perch	River Thames	m	3–8	0.56–0.98	1.75	Williams 1967
		River Thames	f	3–7	0.2–0.64	3.20	[3]Williams 1967
		River Thames	juv	3–5	0.53–1.69	3.19	[3]Williams 1967
					(0.2–1.69)	(8.45)	
Leuciscus leuciscus	dace	River Thames		5–11	0.36–1.31	3.64	[4]Williams 1967
Alburnus alburnus	bleak	River Thames		3–8	0.6–2.4	4.00	[4]Williams 1967
Rutilus rutilus	roach	River Thames		2–11	0.22–1.38	6.27	[4]Williams 1967
		River Stour		3–12	0.44		Mann 1973
					(0.22–1.38)	(6.27)	
Cheilodactylus macropterus	tarakihi	Chatham Islands		5–35	0.03		Vooren 1977
		Chatham Islands		5–22	0.08		Vooren 1977
		New Zealand			0.15		Vooren 1977
					(0.03–0.15)	(5.00)	
II) Exploited Populations:							
Pleuronectes platessa	plaice	North Sea	f	5–13	0.08		Beverton 1964
		North Sea	m	5–13	0.14		Beverton 1964
					(0.08–0.14)	(1.75)	
Brevoortia petronus	gulf menhaden	Gulf of Mexico, Central (1969, 1971)		1–3	0.7–1.6	2.29	[5]Ahrenholz 1981
		Gulf of Mexico, Eastern (1969, 1971)		1–3	0.88–0.98	1.11	[5]Ahrenholz 1981
		Gulf of Mexico, Western (1969, 1971)		1–3	1.17–1.23	1.05	[5]Ahrenholz 1981
		Gulf of Mexico, all areas (1969, 1971)		1–3	0.95–1.2	1.26	[6]Ahrenholz 1981
					(0.7–1.6)	(2.29)	
Gadus morhua	cod	North Sea		0.5–1	0.59–1.46	2.47	[7]Pope and Knights 1982
Coregonus clupeaformis	whitefish	Lake Huron		3.8	0.34–1.67	4.91	[8]Henderson et al. 1983

[1]Increasing with age.
[2]Year to year variation (1946–52); ages 15–23 combined.
[3]Not consistent with age.
[4]Generally increasing with age.
[5]Assuming 20% tag loss rate.
[6]For tag loss rates from 10 to 30%.
[7]8 different years (1967–75).
[8]23 different year classes (1947–75).

As discussed previously, these different estimates can lead to at least as great a difference in results produced by fishery analyses such as yield models or stock reconstruction analyses (Section II).

Reported differences in estimates of M for whitefish stocks living in Shakespeare Lake compared with other relatively small lakes (e.g., Lake McDonald, Table 3) are particularly significant. Because both stocks are of the same species and living in more or less similar environments (small lakes), one might easily (and incorrectly) assume that both have the same rate of natural mortality; but they did not. The lower rates occurred in the stock occupying a small lake with no predators. This is a clear example of the effect that environment, particularly the predator environment, can have on the realized rate of natural mortality in a fish stock. Obviously, choosing a single appropriate constant for this species would be difficult. Choosing an appropriate species-specific constant for some of the other species with multiple estimates might be difficult as well (e.g., rock bass, lake trout, perch, roach, tarakihi, or menhaden, Table 3).

None of these studies from either unexploited or exploited stocks support the assumption that M is constant for any given stock or species, nor are these within-stock ranges particularly narrow. In addition, treatment of the original catch data may have in some cases obscured the "true" variability. Ricker (1947) and Kennedy (1953, 1954, 1963), for example, use a 3-yr smoothing technique to reduce the effects of unequal recruitment; this also serves to reduce variability that may actually be due to differences in natural mortality. Also, single estimates from data collected during only one or two years of sampling (e.g., Wohlschlag 1954; Williams 1967; Mann 1973; Vooren 1977) can be seriously biased by annual changes in either recruitment or mortality rates. If the estimates reported above are even approximately accurate, it is apparent that the range of possible values for M is wide, and that variability can be considerable even within single stocks.

A solution to this problem of choosing a reasonable value for M, at least for long-lived fish, is suggested by the possibility that **variation** in M (not just the mean value) may be related to maximum lifespan. Fish that live for many years must naturally have lower mortality rates than more short-lived fish. These lower rates may also be less variable in the longer lived stocks, if as in many other biological processes, variability is proportional to the mean. This could account for the ubiquity and apparent effectiveness of the constant 0.2 year^{-1}, used almost universally for the long-lived (20 to 30 years) and well-studied fish stocks from northern European seas (e.g., Beverton 1964). If so, assuming a constant M might be valid for these longer lived stocks.

Unfortunately, the few studies cited above do not support this attractive idea. Although in general, mortality rates decease as lifespan increases, the variability in estimates does not appear to follow the same trend. This may be due partially to the relatively similar lifespans (10 to 20 years) for most of the species for which estimates exist. But the apparent range in rates for the shortest lived species cited above (Ahrenholz 1981, *Brevoortia patronus*, ages 1 to 3 years, M range 0.7 to 1.6 year^{-1}) is certainly not greater than ranges reported for the longer lived whitefish (Henderson et al. 1983, *Coregonus clupeaformis*, ages 10+ years, M range 0.34 to 1.67 year^{-1}).

VI. SUMMARY AND RECOMMENDATIONS

Thus it appears that rates of M, or at least rates of M derived by existing estimation methods, do in fact vary widely within many fish stocks. Because the variations appear to be considerable and because the results from fishery models can be sensitive to large variations in M, one must conclude that assuming constancy without proof can have serious consequences for fishery management.

A better approach may be to discard the notion that a single "best" estimate of M can be found, and instead try to tailor estimates of M to local groups, based on some combinations of the methods discussed in Section III. Obviously, practical considerations of time and resources will limit the accuracy and precision with which M can be estimated. Also, the estimates in the studies reviewed here are prone to all the artifacts mentioned in the previous sections. True rates of natural mortality, and their variability, are still very poorly known for even the great stocks of commercial fish in temperature regions that have been subject to continuous exploitation for decades. Careful, repeated tagging experiments probably hold the most promise for determining with any reasonable degree of accuracy, rates of natural mortality in fish stocks. But even these have inherent problems that are not easily

solved. There remains a great need both for new methods, and refinements of the old.

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NATURAL HISTORY OF THE RAYS OF THE GENUS *MOBULA* IN THE GULF OF CALIFORNIA

GIUSEPPE NOTARBARTOLO-DI-SCIARA[1]

ABSTRACT

Mobulid rays, which abound during summer in the southern Gulf of California, southern Baja California, Mexico, were monitored for a period of four years during a study of their biology. A total of 262 specimens belonging to four species of *Mobula* were examined. *Mobula thurstoni* was the most abundant (58% of the catch), followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%). The study area served as a nursery ground for *M. thurstoni*, a summer feeding and mating ground for *M. thurstoni* and *M. japanica*, and a wintering ground for *M. munkiana* and young *M. thurstoni*; *M. tarapacana* was rare. Data on size, weight, sex ratio, life history, seasonality, feeding habits, behavior, habitat, and symbionts are presented for each species. Size segregation was a common feature of *M. thurstoni*, *M. japanica*, and *M. munkiana*; sex segregation was not evident. An extreme degree of feeding specialization was noted: summer prey were almost exclusively the euphausiid *Nyctiphanes simplex*; the mysid *Mysidium* sp. dominated in the winter. A key to the genus *Mobula* in the Gulf of California is presented as an aid for species identification.

This paper reports on natural history aspects of rays of the genus *Mobula* (Mobulidae), a poorly known group of elasmobranchs commonly called manta rays or devil rays, frequent in the Gulf of California. A good early overview of the family Mobulidae was given by Gill (1908). Cadenat (1960) described the natural history of the mobulids of tropical west African waters, based on specimens which were occasionally captured by the local fishermen. However, with the exception of observations carried out with some regularity by Coles (1910, 1913, 1915, 1916a, 1916b) of *Mobula olfersi* (= *M. hypostoma*) and *Manta birostris* off North Carolina, most of the available literature is purely anecdotal and deals with occasionally encountered or harpooned specimens. Long-term field investigations of devil ray ecology and behavior are wanting. As a result, mobulids are among the least known of the batoid taxa. This was recognized by Bigelow and Schroeder (1953) in their comprehensive review of the knowledge of this family. No major contribution to the understanding of any aspect of mobulid biology has since been published.

Regular fisheries for mobulids were not known to exist, because mobulid meat is generally considered of little market value. However, in 1981, during a reconnaissance trip to the southern Gulf of California (Mexico), in the vicinity of La Paz, Baja California Sur, a regular, seasonally important fishery was discovered. This activity afforded the opportunity to study several aspects of the natural history and the ecology of these batoids.

Preliminary oral interviews revealed that local fishermen in the Gulf of California knew of, and routinely captured, four species of devil rays, in addition to the well-known giant manta ray, *Manta birostris*. This information contrasted with the scientific literature, where only two mobulid species, *Manta birostris* and *Mobula lucasana*, were reported for the area (Beebe and Tee-Van 1941; Fowler 1944; Castro-Aguirre 1965). The confusing state of mobulid taxonomy demanded a revisionary work of the genus *Mobula* (Notarbartolo-di-Sciara 1987), and a discussion of the systematics of *Manta* in the eastern Pacific (Notarbartolo-di-Sciara in press). Such effort permitted designation of names for all species of *Mobula* found in the Gulf of California: *M. thurstoni* (Lloyd 1908), of which *M. lucasana* Beebe and Tee Van (1938) is a junior synonym; *M. japanica* (Müller and Henle 1841); *M. tarapacana* (Philippi 1892); and *M. munkiana* Notarbartolo-di-Sciara (1987), which had not been described before. Many of the reports of *M. lucasana* (= *M. thurstoni*) from Central and South America (Beebe and Tee-Van 1941; Fowler 1944; Nichols and Murphy 1944; Barton 1948; Castro-Aguirre 1965; Chirichigno 1974; Pequeño 1983) undoubtedly refer to other species of *Mobula*. A key to the genus *Mobula* in the Gulf of

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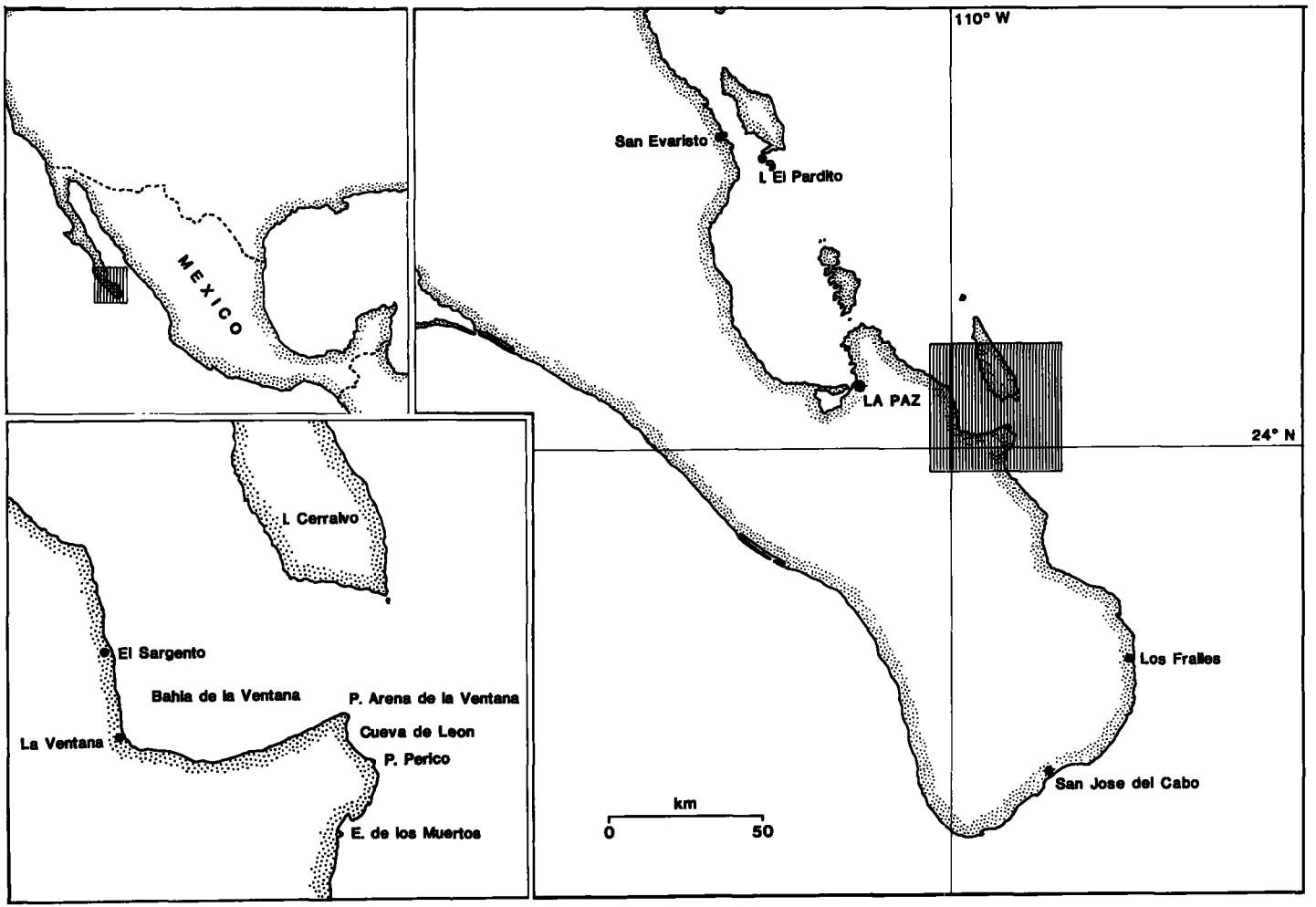

FIGURE 1.—The study area.

California is presented as an aid to future studies of mobulids from this region.

Working relationships were established with the local fishing communities, and their activities were intermittently monitored between 1981 and 1984. Captured rays were examined and measured before their pectoral fins were filleted; stomach contents and reproductive organs were examined later. Information was gathered on size, weight, sex ratios, life history, seasonality, feeding habits, habitat, behavior, and symbionts of four species of rays belonging to the genus *Mobula* (*M. thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*). Detailed descriptions and morphometrics of those species are given by Notarbartolo-di-Sciara (1987). The manta ray, *Manta birostris*, was also occasionally captured (Notarbartolo-di-Sciara in press), but is not treated in the present study.

METHODS

Although mobulids are locally said to be abundant on both sides of the southern Gulf of California, for logistic convenience collecting trips were made only to the peninsular coast (Fig. 1). The fishing cooperative based at Punta Arena de la Ventana was selected as the prime collecting site, because mobulids were caught there more consistently than at other localities. Fishing camps on Isla El Pardito, at Cueva de Leon, Ensenada de los Muertos, and Bahia de los Frailes were also sources of study material. Other fishing communities, such as Juncalito, San Evaristo, El Sargento, La Ventana, and San Jose del Cabo were occasionally visited, but yielded no data because mobulids were not specifically sought by the fishermen. Seven field trips were made. Six were short-term (24 January–8 February 1981, 25 November 1981, 16–21 December 1981, 20–23 December 1982, 19–26 January 1984, and 28 October–1 November 1984); one lasted almost six months (26 January–15 July 1983).

Mobulids of all available species and sizes are caught with nets and harpoon; their meat is filleted out of the pectoral fins for human consumption and used as shark bait. Gill nets are either strung just under the surface or are set on the bottom perpendicular to shore, usually at depths between 10 and 200 m. Fishing vessels were 5–7 m fiberglass launches, locally called "pangas", powered by an outboard engine. Fishing occurred within a radius of about 15 km from a base camp. Nets are checked once a day, early in the morning. Rays weighing up to approximately 100 kg were hauled on board, larger specimens were towed ashore. Rays that were dead in the nets, after several hours (i.e., three unsexed specimens of *Mobula thurstoni*), were often partially destroyed by gammarid amphipods (locally called "plaga"), and were unmarketable.

Specimens were weighed and measured before being processed by the fishermen. Weights (WT) were taken with calibrated spring-scales. Rays lighter than 20 kg were weighed to the nearest pound with a 50-lb scale; weights were subsequently converted to kg. Heavier rays were weighed to the nearest kg with a 150 kg scale. Specimens which exceeded 150 kg (all postnatal *M. tarapacana*) were cut in four pieces and weighed separately. Ten percent was then added to the total weight to compensate for body fluid loss. All the specimens could not be weighed, as occasionally a large number of rays were beached simultaneously, and because of the intense heat the fishermen could not delay their processing.

A set of 29 measurements was taken for morphometric analysis and systematic purposes. Methods and results are presented in Notarbartolo-di-Sciara (1987). Measurements relevant to the present paper were disc width (DW), greatest dimension between outermost tips of pectoral fins, pelvic fin length, from anterior margin of vent to tip of pelvic, and clasper length, from anterior margin of vent to tip of clasper. Most specimens were discarded after measuring and sampling. All preserved specimens were deposited in the Marine Vertebrate Collection of the Scripps Institution of Oceanography. Raw data listing all specimens examined and preserved can be found in Notarbartolo-di-Sciara (1985).

The size and shape of the testes were inspected in male specimens, and the ducti deferentes were cut slightly above the genital papilla. Presence or absence of seminal fluid was determined by running a finger in the caudal direction over the ducts anterior to the cut. Clasper length in thousandths of disc width (DW) was plotted against DW to determine size at maturity, and the presence or absence of seminal fluid was noted. Relative size and contents of uteri and nidamental glands were examined in female specimens, and right and left ovaries were compared. The diameter of the largest ovum was plotted against DW to determine size at maturity of female *Mobula*. Eggs were extracted from the germinative epithelium and their greatest di-

ameter was measured to the nearest 0.1 mm with a steel dial caliper.

Stomach contents, if not larger than approximately 200 cc, were sampled whole; otherwise, the bolus was made homogeneous by stirring, and about 200 cc were preserved. Stomach content samples were fixed and preserved in 10% buffered formalin. The stomach content of each sample was thoroughly agitated, separated with a plankton strainer (mesh size 0.5 mm), rinsed of formalin in deionized water, and blotted for 30 seconds on blotting paper. The lump was then molded into a cylindrical shape, and a portion of one end was separated to make up 1 g of wet weight, measured to the nearest 0.1 g. The subsample was then placed with water in a gridded tray, and examined under a dissecting microscope. Contents of the spiral intestine were discarded, because the small crustacean prey was rapidly digested.

Feeding habits were analyzed quantitatively by computing the Index of Relative Importance (%IRI) (Pinkas et al. 1971; Hyslop 1980) for each prey species. The IRI combines percentage by number (N), mass (M), and frequency of occurrence (F) in the formula:

$$\text{IRI} = (\%N + \%M) \times \%F$$

Prey items were identified, when possible, to lowest taxa or species, then the $\%N$ of all prey species within each subsample was calculated. When more than one species was present, all items were individually counted. To obtain the $\%M$ term of the equation, mean mass was calculated for each species by measuring the length of each item contained in five randomly selected squares on a tray, calculating the average length of each prey species, and obtaining mass values from Miller's (1966) Plankton Conversion Tables, where mass is related to length for all main planktonic taxa. The $\%N$ from all subsamples were summed, and the percent from the new sum was calculated, to calculate %IRI for each prey species. The same procedure was applied to $\%M$ and $\%F$. The total $\%N$ was then added to the total $\%M$, and that sum was multiplied by the total $\%F$, to obtain total IRI for each prey species, from which the %IRI was calculated. When few items (e.g., copepods) were found among a large amount of partially digested euphausiid or mysid shrimps, the possibility of reconstructing the shrimp number within the subsample by counting the digestion-resistant eye pairs was discarded to avoid bias in favor of the shrimp fraction. The following method was adopted instead: all odd prey items were counted and measured, and their total mass was obtained from Miller's tables; this was subtracted from the total weight (1 g) of the subsample. The remaining weight was divided by the mean weight of each individual item, calculated by averaging the lengths of all available intact specimens, and obtaining the corresponding weight in Miller's tables. A potential biasing factor existed, when only a few prey remains were found (e.g., when a relatively uncommon item occurred alone in a stomach, therefore contributing a value of 100 $\%N$ and $\%M$ to the total IRI). This factor was avoided by considering, for quantitative treatment, only those stomachs which contained more than 1 g (wet weight) of recognizable food. All stomachs that had <1 g of contents were in fact virtually empty, and the few items found in them were treated only qualitatively.

Remoras were fixed in 10% formalin, preserved in 50% isopropanol, and deposited in the Marine Vertebrate Collection, Scripps Institution of Oceanography. Parasitic copepods were fixed and preserved in 50% isopropanol and sent to the Long Beach State University for taxonomic identification and study.

RESULTS AND DISCUSSION

A total of 262 mobulid rays, belonging to four species (*Mobula thurstoni*, *M. japanica*, *M. munkiana*, and *M. tarapacana*) were examined between 1981 and 1984. Of these, *M. thurstoni* was the most abundant species, constituting 58% of the total catch, followed by *M. japanica* (30%), *M. munkiana* (9%), and *M. tarapacana* (3%).

KEY TO THE SPECIES OF *MOBULA* IN THE GULF OF CALIFORNIA

Mobula can be distinguished from *Manta* by the mouth on the lower surface of the head rather than being subterminal, and by the presence of toothbands in both jaws. Moreover, *Manta* grows to a greater size, and the size of its head, relative to the body, is much greater than in *Mobula*.

1a. Branchial filter plates fused .... *M. tarapacana*
(Spiracle in an elongated longitudinal slit, dorsal to plane of pectoral fins. Teeth tessellated, surface of crown pitted, buccal edge comblike. Thick cover of acumi-

nate denticles. Large adult size, often exceeding 3 m in width. Dorsal side greenish brown. Ventral side anteriorly white, posteriorly gray).

1b. Branchial filter plates separate 2

2a. Spine on base of tail ..... *M. japanica* (Tail very long with a line of white tubercles on both sides. Spiracle a short transversal slit, dorsal to plane of pectoral fins. Teeth not in contact with each other, at least twice as high as the crown is wide; crown subtriangular in apical view. Medium-large adult size, approaching 2.5 m in width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white. Skin rough to the touch).

2b. No spine on base of tail ..... 3 (Spiracle small, subcircular, ventral to plane of pectoral fins. Skin smooth to the touch).

3a. Base of tail dorsally depressed .... *M. thurstoni* (Double curvature of anterior margin of pectoral fin. Surface of tooth crown rugose. Medium adult size, exceeding 1.8 m of width. Dark blue to black on dorsal side, apex of dorsal fin white; ventral side white, with a dark greenish patch near the posterior margin of each pectoral fin, and with a pattern of dark and shiny silvery pigmentation on distal half of pectorals).

3b. Base of tail laterally compressed .... *M. munkiana* (Anterior margin of pectoral fin straight to weakly convex. Surface of tooth crown smooth. Small adult size, barely exceeding 1 m of width. Dorsum mauve gray; ventral side white, tips of pectoral fins gray).

Mobula thurstoni (Lloyd 1908)
Local name: cubana de lomo azul

Eighty one males (disc width range 630–1,770 mm), 69 females (210–1,801 mm), and three specimens of undetermined sex (941–1,494 mm), were caught at four stations (Punta Arena de la Ventana, Cueva de Leon, Ensenada de los Muertos, and Isla El Pardito) and their adjacent waters, between 7 February 1981 and 30 October 1984. Overall and seasonal size-frequency distributions for *M. thurstoni* are given in Figure 2. Mean size varied with season, smaller rays being dominant in winter catches, medium sizes prevailing in the summer. The difference between mean disc width (DW) in winter and overall mean DW is highly significant (T-value = 5.189, df = 169, $P << 0.001$). There were no significant differences between male and female DWs (T-value = 0.3767, df = 145, $P > 0.5$), with the exception of the November to February period, when females were larger (T-value = 2.331, df = 12, $P < 0.05$).

A total of 105 specimens (210–1,770 mm DW) were weighed. The WT/DW relationship is best described by the equation:

$$WT = 4.817 \times 10^{-8} (DW)^{2.78}$$

$$r = 0.99$$

WT is given in kg, DW in mm. The largest specimen in the sample was a female; DW was not measured because the fishermen had already started filleting the pectoral fins. Calculated DW, regressed from disc length, cranial width, and upper toothband length, was 1,801 mm (multiple correlation coefficient = 0.99). The second largest specimen was also a female, 1,799 mm DW. The largest male had a DW of 1,770 mm and weighed 53 kg. The smallest freshly caught specimen was 876 mm DW and weighed 6.4 kg. The smallest postnatal specimen was a male, the carcass of which was found drying on the beach in Ensenada de los Muertos. Its calculated DW, regressed from toothbands length, was 864 mm (multiple correlation coefficient = 0.99).

Overall ratio of males to females caught was 1.18 (N = 148). Catch sex ratios varied with season. Females appeared to be dominant in winter (ratio of males to females 0.27; N = 14). The reverse was true in March, in favor of males. A significant difference from a 1:1 ratio (chi square test $P > 0.05$) was not noted. Geographical segregation, either of sex or size, was not apparent for *M. thurstoni* during the warmer months when a wide array of size classes and both sexes were found in the same fishing area. Males and females were occasionally harpooned from the same group basking at the surface. This fact argues against behavioral sex segregation. Winter data, however, were suggestive of size segregation at that time of year. It was common knowledge among local fishermen that during the winter months all *M. thurstoni* caught are small. The bimodal size-frequency distribution for early

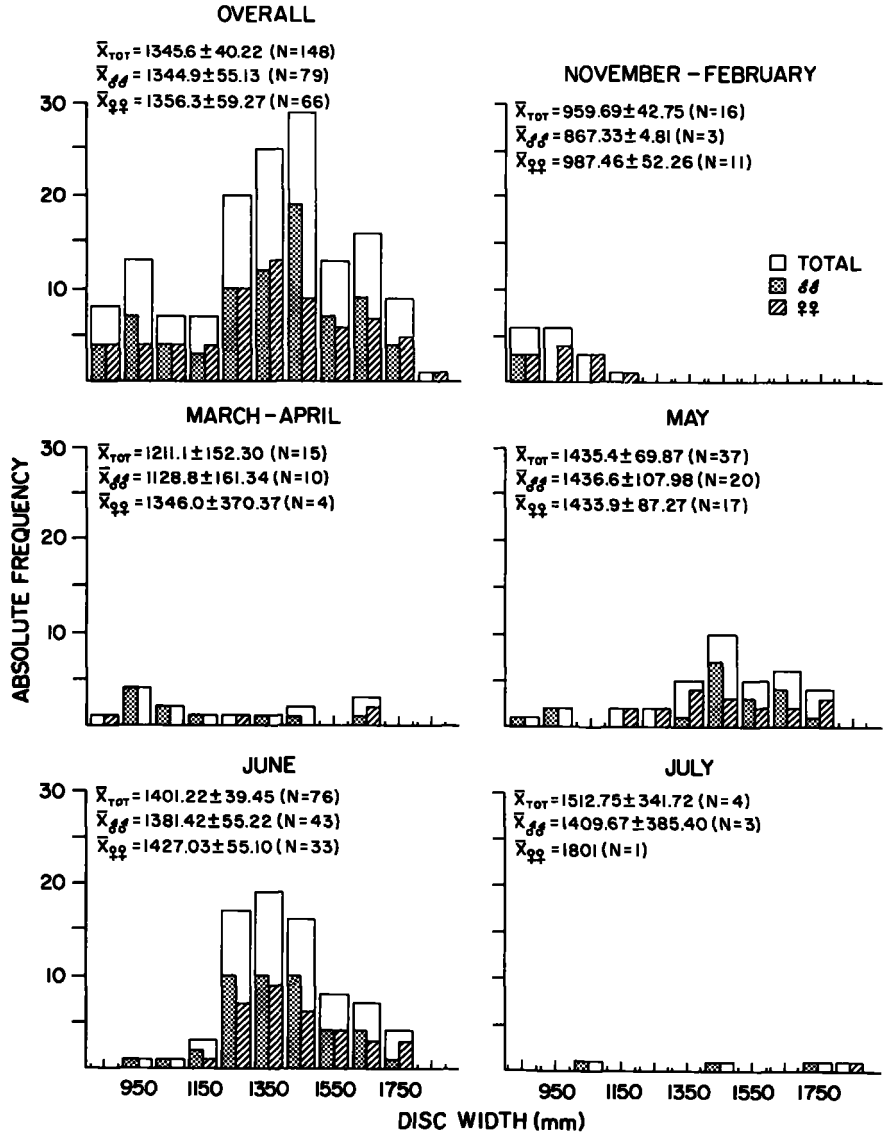

FIGURE 2.—Size-frequency distributions of *Mobula thurstoni* (means ±2 SE).

spring (Fig. 2) suggested that larger rays began to move into the area in the spring from their unknown wintering grounds.

Mature testes are large, elongated structures attached by the mesorchia to the upper anterior wall of the pleuroperitoneal cavity, on either side of the vertebral column. A large epigonal organ is associated with each testis. Both testes appeared to be functional. They were usually about the same size, although occasionally the left testis was nearly 25% larger. The paired ducti deferentes remain separated from each other throughout their length and open into the cloaca at the tip of the urogenital papilla through two distinct pores, rather than merging in the urogenital sinus, as in most elasmobranchs (Daniel 1934), including *Manta ehrenbergi* (Gohar and Bayoumi 1959). Clasper length was plotted against DW for 43 *M. thurstoni* (Fig. 3), to determine the onset of male maturation. Rapid increase in relative size of the claspers, beginning at a DW of about 1,500 mm, was concomitant with the incipient presence of abundant seminal fluid in the lower portion of each ductus deferens. The pelvic fin area, and

especially the tissue at the bases of claspers, of the larger males appeared swollen and congested in May and June, and some of the skin had assumed a pink coloration. Similar observations in carcharhinid and odontaspid sharks have been linked with mating activities (Springer 1960; Gilmore et al. 1983).

The ovaries in *M. thurstoni* are paired, elongated organs located inside the pleuroperitoneal cavity, analogously to the testes, and are connected to a large epigonal organ. Eggs are produced within the germinative epithelium. The largest eggs were found at the anterior end of the ovary. Only the left ovary develops and is functional, whereas the size and aspect of the right ovary remains comparable with those of the immature stage. Asymmetry is also present in the oviducts, the left uterus being usually the largest in mature females. It consists of a voluminous, thick-walled expansion of the lower tract of the oviduct; its lumen is lined with a highly developed epithelium consisting of elongated, flattened villi (trophonemata), a well-known mobulid (Gill 1908; Setna and Sarangdhar 1950; Wourms 1977) and rhinopterid (Schwartz 1966; Smith and Merriner 1986) feature. In several instances both uteri were found to contain a viscous, whitish or greenish substance. Oviducts open separately into the cloaca. A progression of sexual maturity in female mobulids was evident from the examined ovary's developmental condition. In the immature female the germinative epithelium is a narrow, leaf-shaped band, tapering at both ends, located opposite to the mesovarium (facing the center of the cavity) along the ovary's longitudinal axis. In mature females the germinative epithelium takes over most of the ovary's ventral side, making room for the mature ova. To determine the size at maturity of female *M. thurstoni*, the diameter of the largest ovarian egg was plotted against DW (19 specimens, Fig. 4). An egg growth plateau was not evident, because data on

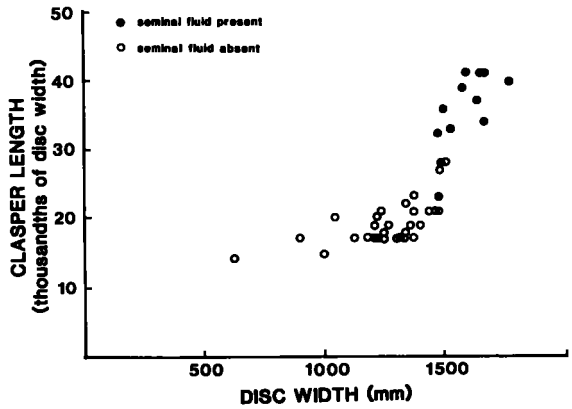

FIGURE 3.—Relationship between clasper size and body size in *Mobula thurstoni*.

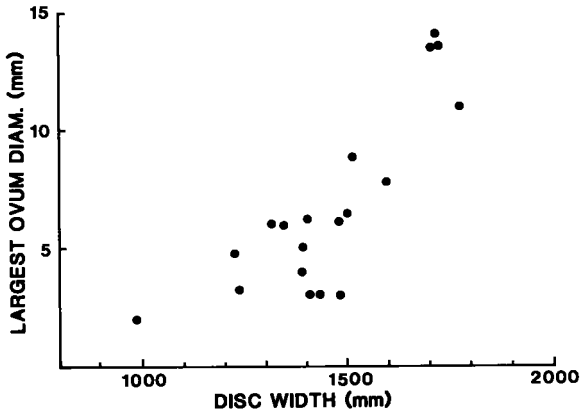

FIGURE 4.—Relationship between size of largest ovum and body size in *Mobula thurstoni*.

the larger sizes were insufficient, and therefore the maximum egg diameter was not known. It appears from the scanty available data that female *M. thurstoni* began to mature at a DW of about 1,500 mm (the point at which the slope of the curve becomes steeper).

Mobula thurstoni, like all mobulids, is a viviparous matrotroph (Wourms 1981), the near-term embryo being three orders of magnitude larger than the mature egg. Uteri and nidamental glands of 68 females were inspected. No adult female examined from March through June (N = 55) was pregnant. Embryos were found in July and October. Two embryos from females caught in July were near-term. Four embryos found in October were in an early stage of development. All females (N = 4) inspected in October were pregnant, and all embryos were in the same developmental stage, suggesting coordinated breeding activity. The largest female (DW 1,801 mm) had a single embryo, which appeared to be in the final stage of fetal development, fully pigmented, the yolk sac completely absorbed, and the umbilicus a mere scar (Fig. 5A). The embryo's DW was 630 mm; its WT, 3.4 kg. It occupied the left uterus with the rostrum pointed forward. Its pectoral fins were folded dorsally, the right pectoral on top. The cephalic fins were almost totally unrolled and extended ventrally towards the midline of the body. The uterus, with the embryo inside, occupied roughly one third of the female's pleuroperitoneal cavity. Lack of space inside the cavity and the distended skin on the abdomen made it apparent that no other embryo had been recently expelled or aborted. Uniparity appears to be a common pattern within the genus *Mobula* (Hill 1862; Gill 1908; Coles 1913, 1916b; Barnard 1925; Setna and Sarangdhar 1950; Cadenat 1960; Wallace 1967; Capapé and Zaouali 1976; Figueiredo 1977). Only Risso (1826) asserted that *Cephaloptera giorna* (= *M. mobular*) may have one or two young, but his statement was not documented. Since the smallest free-swimming specimen noted had a DW of 864 mm, the average size at birth for *M. thurstoni* is probably between 650 and 850 mm DW, and a WT of approximately 4.5 kg. The second largest female (DW 1,799 mm) had also only one embryo in her left uterus. The embryo was unpigmented, with disc 210 mm wide, and weighed 173 g. Like the term-embryo, its rostrum was pointing forward; unlike it, however, its pectoral fins were folded ventrally.

Mating, parturition, and early mobulid life history take place in the shallower portion of a population's range, not an uncommon elasmobranch feature. McLaughlin and O'Gower (1971) discussed inshore movements in the mating Port Jackson shark *Heterodontus portusjacksoni*, as did Springer (1960) for the sandbar shark *Eulamia milberti* (= *Carcharhinus plumbeus*). One-year-old gray reef sharks, *Carcharhinus amblyrhynchos*, were observed in French Polynesia in shallower waters than adults by Nelson and Johnson (1980). A similar result was reported for the hammerhead shark, *Sphyrna lewini*, by Clarke (1971) in Hawaii and by Klimley (1983) in the Gulf of California. Bullis (1967) hypothesized an upward movement to shallower depths for newborn marbled cat sharks, *Galeus arae*. There is likely an advantage for juveniles to remain in relatively protected areas during the earlier stages of their life, when they are most vulnerable to predation (Springer 1967).

Examination of 139 stomachs indicated that *M. thurstoni* was extremely specialized in its feeding habits. Eighty one (58.3%) stomachs were empty, or had only traces of food (<1 g wet weight). The remaining 58 stomachs (41.7%) had quantifiable contents. All recognizable prey items were planktonic crustaceans (with the exception of a few fish eggs, one nematod, and a small coleopteran, probably ingested accidentally when it was floating). They were listed, ranked by decreasing %IRI, in Table 1. *Mobula thurstoni*

TABLE 1.—Prey species found in 57 stomachs of *Mobula thurstoni*, ranked by decreasing Index of Relative Importance (IRI). N = percentage of prey species by number; M = percentage of prey species by mass; F = percent frequency of occurrence of prey species.

Prey species	N	%N	M	%M	%F	IRI	%IRI
Nyctiphanes simplex	4,940.8	86.70	4,982.0	87.40	87.7	15,268	97.90
Mysidium sp.	635.2	11.10	631.2	11.10	12.3	273	1.75
Copepoda	99.9	1.80	74.5	1.31	15.8	49	
Megalopa larvae	12.0	0.21	4.1	0.07	14.0	3.95	
Hyperiid amphipods	6.8	0.12	5.8	0.10	5.3	1.18	0.35
Fish eggs	1.4	0.03	1.8	0.03	5.3	0.302	
Nematoscelis diff.	0.5	0.01	1.1	0.02	1.8	0.050	
Stomatopod larvae	0.7	0.01	0.6	0.01	1.8	0.041	

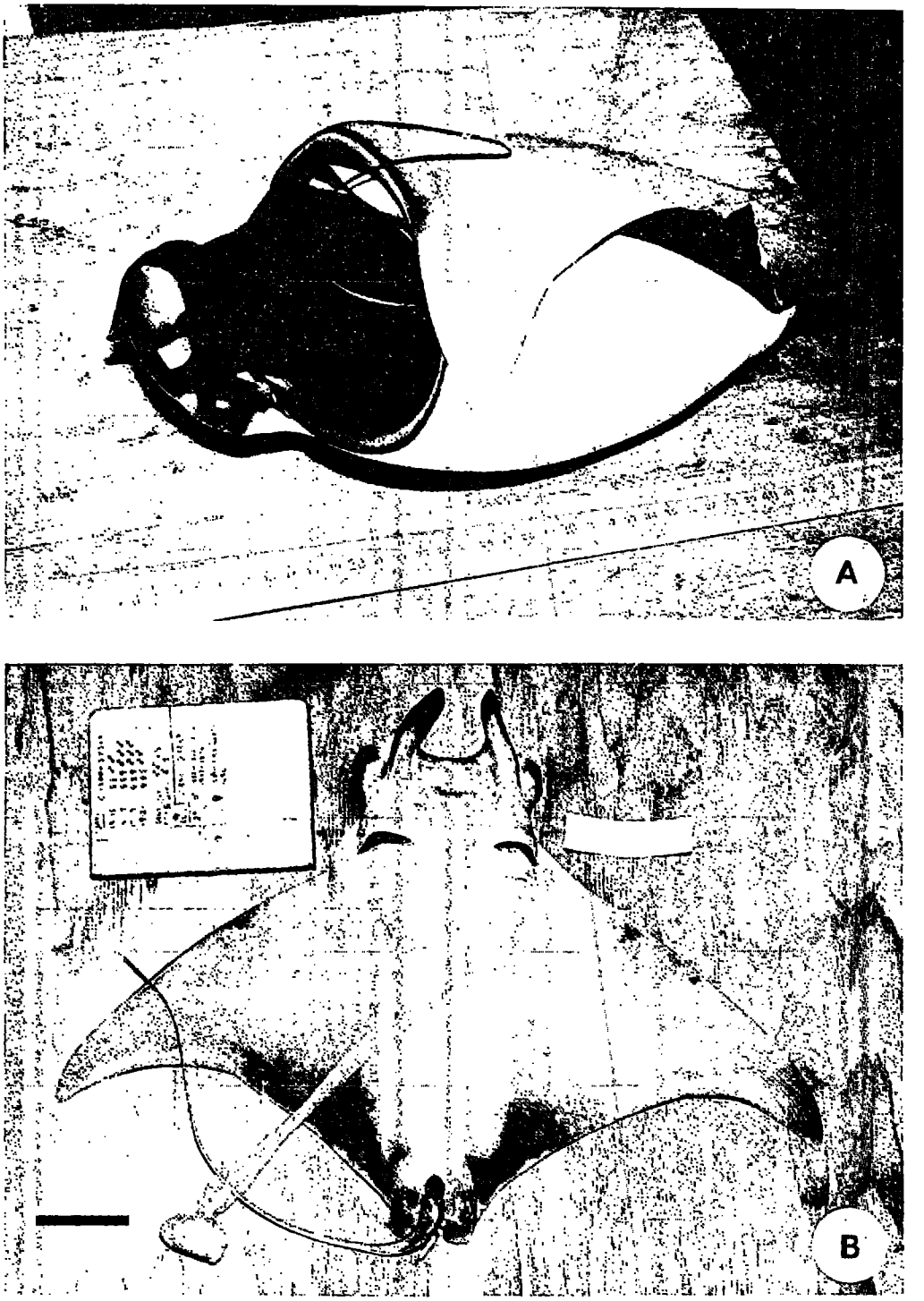

FIGURE 5.—A: term-embryo of *Mobula thurstoni*. The scale in the photograph is in centimeters. B: embryo of *M. tarapacana*. The scale bar equals 5 cm.

fed mostly on adult and juvenile euphausiids, *Nyctiphanes simplex*. The mysid *Mysidium* sp. (underscribed, Thomas E. Bowman[2]) was second in order of importance. Mysids and euphausiids were never found together in the same stomach. The overall importance of the two food items differed by two orders of magnitude. All other prey species found in the stomachs were rare and probably fortuitously ingested. These included one zoea larva and the following copepod species: *Undinula vulgaris*, *Eucalanus subcrassus*, *E. subtenuis*, *Temora discaudata*, *Scolecithrix danae*, *Nannocalanus minor*, *Euchaeta remana*, *Euchaeta* sp., and *Labidocera diandra*. Diet varied with season (Fig. 6A), with mysids being dominant from December through March, and euphausiids during the warmer months. Diet varied with predator size (Table 2): smaller individuals fed both on euphausiids and mysids; the larger rays fed only on euphausiids. This result probably reflects the predominance of smaller rays during winter, when fewer euphausiids are available, rather than an ontogenetic change in food preferences.

TABLE 2.—Size differences in the diet of *Mobula thurstoni*.

	%IRI	
Prey species	DW < 1,300 mm (n = 21)	DW > 1,300 mm (n = 36)
Nyctiphanes simplex	79.04	99.91
Mysidium sp.	18.13	0
Other	2.83	0.09

Two remoras (Echeneididae) were occasionally found on large *M. thurstoni*: *Remora remora* (3 specimens; range: 98–200 mm SL), and *R. albescens* (3 specimens; 93–100 mm SL). Crustacean parasites were encountered: *Pupulina minor* (Copepoda: Caligidae), *Ecthrogaleus denticulatus* (Copepoda: Pandaridae) sparsely on the skin, and *Ecthrogaleus disciarai* (Benz and Deets 1987) in large patches on the dorsal surface, *Entepherus laminipes* (Copepoda: Cecropidae) from the branchial filter plates, *Eudactylina oliveri* (Copepoda: Eudactylinae) from the gill lamellae, and *Kroeyerina* sp. (Copepoda: Kroyeriidae) from the olfactory lamellae.

Mobula thurstoni was usually observed at the surface in coastal waters of Bahia de la Ventana, Cueva de Leon, and Bahia de los Muertos, often within a few hundred meters of land and occasionally as far as 6 km. When sighted offshore, it was sometimes found over considerable depths (>500 m), although it appeared to be more abundant in shallower, neritic waters. *Mobula thurstoni* was always caught in the shallower part of the nets, usually at a depth of <100 m. The greatest part of the catch, however, was surface-dwelling rays. Beginning in mid-April, numerous *M. thurstoni* were consistently seen in the early morning hours cruising slowly at the surface. They would frequently pause, conspicuous on calmer days, with the tips of their pectoral fins protruding out of the water. This behavior is well known in mobulids (Norman and Fraser 1937); it has been observed also in connection with mating activities in *M. olfersi* (= *M. hypostoma*) by Coles (1910). During such occasions, fishermen could easily approach the rays and harpoon them, before startling them and causing them to dive. Repeated captures within the same aggregation revealed that rays of various sizes and both sexes could be found together. While at the surface, *M. thurstoni* was usually solitary or in small, nonpolarized groups (2–6), rather than in larger aggregations or schools. The species was frequently seen jumping out of the water in spectacular, often reiterated somersaults; it was recognized by the distinctive ventral markings.

It is not known to what extent mobulids make use of the sea bottom. Beebe and Hollister (1935) observed a group of 12 small devilfish (most likely *Mobula*) lying on the sandy substrate off Frigate Islet, in the British West Indies. Bigelow and Schroeder (1953) speculated that *Manta* spends much of its time resting quietly on the seafloor. During an experiment organized in conjunction with Sea World of San Diego, aimed at establishing whether *M. thurstoni* could survive in a confined environment, five young specimens were captured with gill nets and kept in a large pen (6 m in diameter) anchored in 2.5 m of water in Ensenada de los Muertos. None of the rays survived 24 hours of captivity; the reasons for their deaths were not clear, although the particularly stressful capturing method appeared as a likely cause. During that experiment the negatively buoyant rays (sinking tail-first as soon as they stopped swimming) spent a great deal of time resting on the bottom, and were able to circulate water through their gills while resting, by a synchronized maneuvering of the oral valve and of the gill covers (as judged from the flow made visible by the numerous particles suspended in the water). A frequent method of turning around

[2]Thomas E. Bowman, Smithsonian Institution, Washington, D.C., pers. commun. 1984.

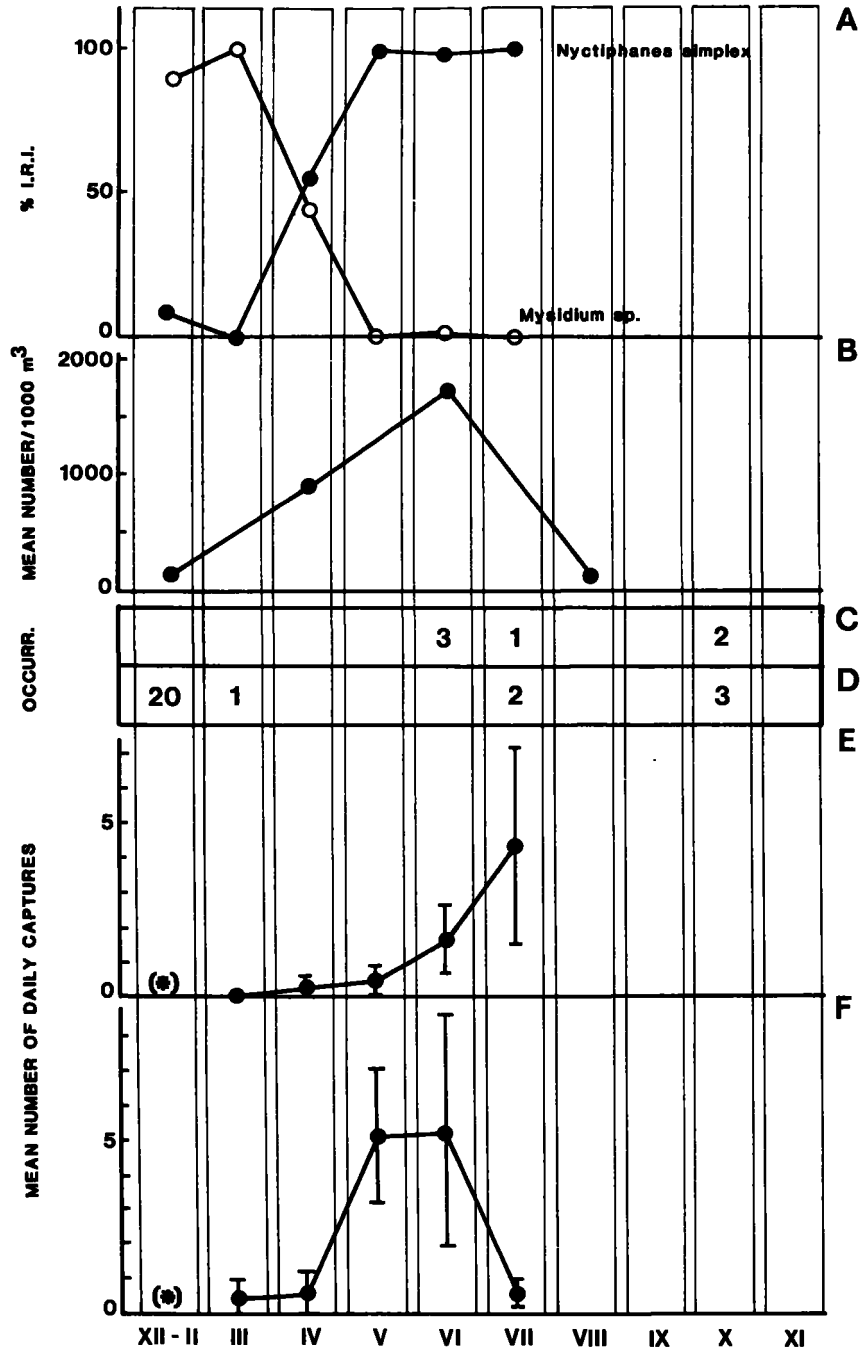

FIGURE 6.—A. seasonal variation of the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *Mobula thurstoni*. B. seasonal variation of the abundance of adult and juvenile *N. simplex* in the coastal areas of the southwestern Gulf of California (modified from Brinton and Townsend 1980). C. captures of *M. tarapacana*. D. captures of *M. munkiana*. E. mean number of daily captures of *M. japanica*; bars represent 2 SE on either side of the mean. F. mean number of daily captures of *M. thurstoni*; error bars as in E. (*): although specimens were also captured between December and February, data are not comparable with spring and summer captures because catch effort was minor and inconsistent in the colder months.

(e.g., when swimming towards the wall of the pen) was to dive vertically in a tight circle until swimming in the opposite direction in an inverted position, and then spinning around the body axis to bring the dorsal side up, rather than turning by banking to the right or to the left.

An indication of the seasonal abundance of *M. thurstoni* in the surface waters of the study area was obtained by the mean number of rays caught daily from March to July 1983 (Fig. 6; Table 3). Mean daily catch should be taken as a rough indication of the relative abundance of *M. thurstoni* rather than as a precise index because the fishing effort was difficult to quantify. Mean effort, however, was roughly constant from March through July because the mean monthly number of working boats (about 20) and the number and size of the nets set then was constant. Furthermore, the fishermen would harpoon a ray every time they had the opportunity to do so. Peak of abundance was in June, a result which appears to be consistent with the fishermen's past experience, despite the 1983 abnormally high water temperatures (Cane 1983). In July the number of *M. thurstoni* caught had dropped drastically, and most of the catch consisted of *M. japanica*. No information was obtainable for the August–September period. Eighteen specimens were captured during six fall and winter field trips (24 January–8 February 1981; 25 November 1981; 16–21 December 1981; 20–23 December 1982; 19–26 January 1984; 28 October–1 November 1984), but that figure was not comparable with other data because part of the fishing cooperative migrated south to Los Frailes during the cooler months. It is common knowledge, however, among the local fishermen, that *M. thurstoni* in the colder season is present, but in fewer numbers than during the summer.

The study area constitutes a feeding, mating and nursery ground for *M. thurstoni*. The euphausiid *Nyctiphanes simplex*, the main diet item and the only food of the adults when in the area, is the most abundant and widespread euphausiid in the Gulf of California, and has been observed in dense swarms (Brinton and Townsend 1980). Although it is found in the study area year-round, its juvenile and adult stages are most abundant between February and August, peaking in June on the west side of the Gulf of California (Brinton and Townsend 1980). The seasonal abundance of *M. thurstoni* in the southern Gulf thus seems to be closely related to the seasonal abundance of its main prey. It is impossible to describe the general movement and life history pattern of *M. thurstoni* in the Gulf of California from the fragmentary information available. The scanty data, however, suggest the following: 1) adult male and nonpregnant adult female *M. thurstoni* enter the area in spring to feed and to mate, 2) pregnant females segregate from the rest of the population in spring (as is also suggested by the slight predominance of males in spring and early summer), 3) gestation period is one year and females give birth to one young every two or more years, 4) the young are born in the study area or near it in midsummer and remain there throughout their early life, and 5) in late summer, when the numbers of adult and juvenile *Nyctiphanes simplex* decline due to intense heating of the water (Brinton and Townsend 1980), adult *M. thurstoni* leave the area, whereas the young switch their diet from euphausiids to mysids. Further investigations are needed for additional corroboration of these hypotheses.

TABLE 3.—Mean number of daily captures of *Mobula thurstoni*. a = total monthly number of captures; b = monthly number of days of monitoring; $\bar{X}$ = mean number of daily captures; SE = standard error of the mean; SD = standard deviation.

Month	a	b	$\bar{X}$	2SE	SD	range
March	6	16	0.38	0.54	1.1	0–4
April	9	13	0.69	0.69	1.3	0–4
May	35	7	5.00	1.95	2.6	1–9
June	77	15	5.10	3.32	6.4	0–23
July	5	9	0.56	0.34	1.0	0–3

Mobula japanica (Müller and Henle 1841) Local name: cubana de lomo blanco

A total of 78 specimens, 34 males (DW range 1,316–2,386 mm) and 44 females (1,470–2,302 mm), were caught at three stations (Punta Arena de la Ventana, Cueva de Leon, and Ensenada de los Muertos) and adjacent waters, between 16 December 1981 and 13 July 1983. Overall and seasonal size-frequency distributions for *M. japanica* are shown in Figure 7. With the exception of April, when females were larger (T-value = 4.697, df = 3, $P < 0.02$), there are no significant size differences between the sexes (T-value = 0.535, df = 76, $P > 0.5$). Most of the rays in the sample were large; only three were <1,900 mm DW.

Twenty-seven specimens (size range: 1,316–2,285 mm DW; 18.6–115 kg) were weighed. The WT/DW relationship is described by the equation:

$$WT = 4.29 \times 10^{-10} (DW)^{3.4}$$

$$r = 0.98$$

where WT is given in kg, DW in mm. The overall male to female ratio was 0.89 ($N = 78$). Females dominated the June through December period; males were predominant in April and May. Sex ratios, however, never significantly differed from 1 (χ^2 test $P > 0.05$). Sex segregation, behavioral or geographical, was never observed in *M. japanica* (both sexes were caught together in nets and by harpoon); sampling bias ($N = 3$) may explain why only males were caught in May. Geographical size segregation, by contrast, was an evident feature of sexually mature specimens in the Gulf of California (Fig. 7).

No pregnant females were found, although in some specimens the left uterus had a flabby and dilated appearance, suggesting recent delivery. Tissues at the base of the claspers of most of the larger males were swollen and reddened in June and July when the tips of the claspers were flexible and the rhipidion could be easily spread, and in doing so a white, viscous fluid would ooze from the hypophyle; all this suggested mating activity. The clasper length-DW relationship for *M. japanica* (Fig. 8) did not exhibit a clear pattern as in *M.*

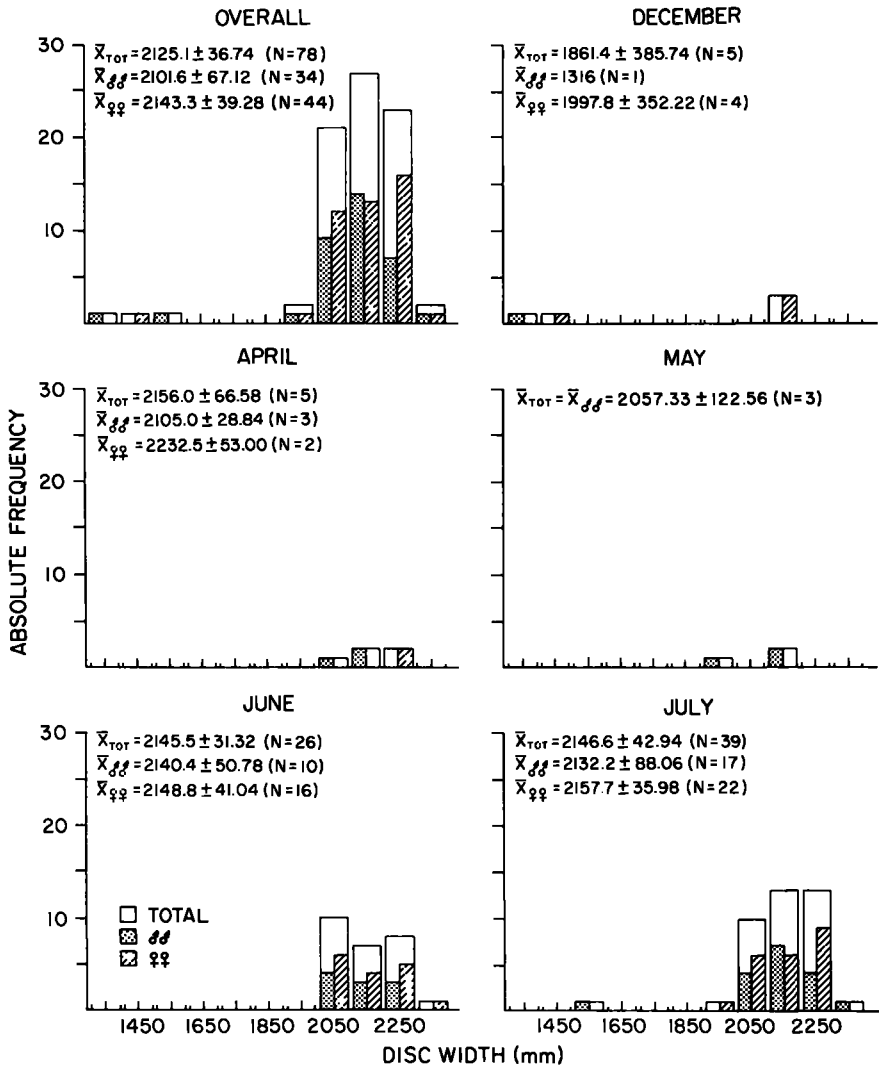

FIGURE 7.—Size-frequency distributions of *Mobula japanica* (means ±2 SE).

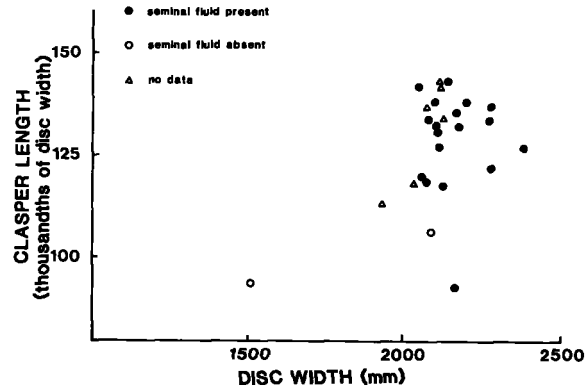

FIGURE 8.—Relationship between clasper size and body size in *Mobula japanica*.

thurstoni, since most of the specimens of *M. japanica* were of larger size classes. It was apparent, however, that at a DW between 2,050 and 2,150 mm there is a high degree of variability in the relative size of claspers, which tended to stabilize at higher values (DWs >2,150 mm), indicating that male sexual maturity in *M. japanica* begins at a DW of 2,100 (±50) mm. Lack of information on smaller specimens prevented a clear understanding of the onset of female sexual maturity (Fig. 9). Large eggs were found in specimens as small as 2,070 mm DW, possibly indicating that female *M. japanica* began to mature at that size.

Only 19 (24%) of 78 specimens had quantifiable stomach contents (>1 g wet WT). The remaining 59 stomachs (76%) were empty or had only traces of food. All *M. japanica* fed largely on the euphausiid *Nyctiphanes simplex* (Table 4); no mysids were found. Other species occurring in the stomachs, including copepods, megalopa larvae, stomatopod larvae, hyperiid amphipods, caridean decapods (*Crangon* sp., *Pasiphaea* sp., and one alpheid decapod), and one cumacean, had an overall relative diet importance of only 0.38%. *Mobula japanica* were therefore very similar in feeding habits to large *M. thurstoni*. Information on the

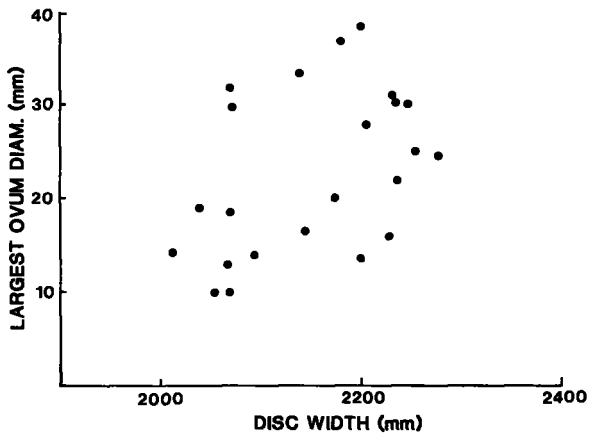

FIGURE 9.—Relationship between size of largest ovum and body size in *Mobula japanica*.

TABLE 4.—Prey species found in 19 stomachs of *Mobula japanica*, ranked by decreasing Index of Relative Importance (symbols as in Table 2).

Prey species	*N*	%*N*	*M*	%*M*	%*F*	IRI	%IRI
Nyctiphanes simplex	1,890.64	99.51	1,869.85	98.41	100.00	19,792	99.62
Copepoda	4.61	0.24	1.15	0.06	31.58	9.47	0.05
Other	4.74	0.25	29.00	1.53	36.84	65.58	0.33

winter diet of *M. japanica* was lacking, as four of the five specimens collected then had empty stomaches; the fifth, a large female, contained a small fragment of a partially digested fish carcass. Since quantifiable stomach contents were found only in large rays between April and July, no size or seasonal differences in the diet of *M. japanica* could be detected.

Mobula japanica was often found carrying *Remora remora*, usually seen clinging to the outside of body, but found once inside a spiracle. Six specimens of *R. remora* (range 109–217 mm SL) were collected from *M. japanica*. Only one specimen of *R. albescens* (97 mm SL) was found, in the mouth cavity of a *M. japanica*. A pilot fish, *Naucrates ductor* (Carangidae) also associated with *M. japanica*, swam alongside a harpooned ray that was being towed inshore and remained for some time at the water's edge, where the ray was beached. *Mobula japanica* was parasitized by the following crustaceans: *Nerocila acuminata* (Isopoda: Cymothoidae), *Pupulina brevicauda* and *P. minor* (Copepoda: Caligidae) on the skin; *Eudactylina oliveri* (Copepoda: Eudactylinae) in the gills; and *Kroeyerina* sp. (Copepoda: Kroyeriidae) among the olfactory lamellae. Unidentified trypanorhynch cestodes were occasionally found within the pleuroperitoneal cavity.

Habitat preference of *M. japanica* did not appear to differ from that of *M. thurstoni*. However, the use of the habitat differed seasonally: in April and May, when *M. thurstoni* was abundant at the surface, *M. japanica* was never seen, and few specimens were bottom gillnetted during those months. Conversely, *M. japanica*, in June and July, was seen in the late morning hours at the surface in groups of several individuals swimming parallel to the shore. Occasionally specimens were seen in water <1 m deep. *Mobula japanica* is not known to school, and I never observed schooling.

Coles (1910) reported that *M. olfersi* (= *M. hypostoma*) utters a "musical, bell-like bark" when dying. A similar account was given by Risso (1810) of *Cephalopterus massena* (= *M. mobular*). This information led subsequent authors (Norman and Fraser 1937; Bigelow and Schroeder 1953) to wonder whether mobulid rays are capable of producing sounds while in the water. Sound production is a fairly widespread phenomenon among bony fishes (Fish and Mowbray 1970; Tavolga 1971); however, elasmobranchs lack the traditional structures used by teleosts to generate sound, i.e., the swim bladder and bony skeletal parts (Marshall 1962), and recognizable sounds have not been recorded from these animals (Backus 1963). Sound production among elasmobranchs has been reported only for the Atlantic cownose ray, *Rhinoptera bonasus* (Myrberg 1981); in that case clicks and scraping sounds were presumably produced with the dental plates, elicited when strongly prodding three rays which were confined in a tank (Fish and Mowbray 1970). *Mobula japanica*, when beached alive, often emitted a distinctive noise which could have been the equivalent of Coles' "bark". This noise, however, was apparently caused by the periodic, spasmodic contractions of the mandibular, pharyngeal, and hypobranchial musculature of the asphyxiating ray, which forced air from the mouth cavity out of the gill openings through the meshlike branchial filter plates. Although underwater sonic recordings have never been made, it seems unlikely that under normal circumstances any audible sound could be produced in this fashion by submerged mobulids.

This area served as a spring and summer feeding and mating ground for adult *M. japanica*, rather than as a pupping or nursery ground, as indicated by the lack of small-sized specimens. Seasonal abundance of *M. japanica* in the surface waters was indicated by the catch data (Table 5) and is comparable to the seasonal abundance of *M. thurstoni* (Fig. 6). No *M. japanica* were observed in March; in April and May they occurred occasionally. By mid-June large numbers appeared in the nearshore surface waters near Punta Arena de la Ventana, and were easily harpooned. Most of the July mobulid catch consisted of *M. japanica*, when the numbers of *M. thurstoni* had declined. Data are lacking for the August–October period, therefore it was impossible to tell whether the peak of abundance occurred in July or later. Fishermen's reports were not clear, although there was agreement on an overall decline of mobulid abundance in late summer. *Mobula japanica* fed exclusively on the euphausiid *Nyctiphanes simplex*, and its numbers apparently declined concomitant with the late summer decline

TABLE 5.—Mean number of daily captures of *Mobula japanica* (symbols as in Table 1).

Month	*a*	*b*	$\bar{X}$	2 SE	SD	range
March	0	16	0	0	0	0–0
April	5	13	0.4	0.36	0.7	0–2
May	3	7	0.4	0.40	0.5	0–1
June	26	15	1.7	1.02	2.0	0–6
July	39	9	4.3	2.89	4.3	0–14

of abundance of their prey (Brinton and Townsend 1980). Some *M. japanica*, however, including individuals both large and small, were found in this region throughout December. Like *M. thurstoni*, winter catch data are not comparable because of differences in fishing effort, when *M. japanica* is apparently caught less frequently.

Mobula munkiana Notarbartolo-di-Sciara 1987 Local name: tortilla

Twenty-four specimens, 10 males (DW range 686–900 mm) and 14 females (719–1,097 mm), were caught at four stations (Punta Arena de la Ventana, Ensenada de los Muertos, Bahia de los Frailes, and Isla El Pardito) and adjacent waters, between December 1982 and October 1984. Size-frequency distributions for *M. munkiana* (Fig. 10) revealed that female mean size was greater than male, although not significantly (T-value = 1.724, df = 22, $P > 0.1$). Seasonal differences in size-frequency distribution could not be examined because *M. munkiana* were only collected during the fall and winter. All 10 freshly captured specimens were weighed (size range: 686–1,097 mm DW; 4.1–11.8 kg). Their WT/DW relationship is described by the following equation:

$$WT = 1.041 \times 10^{-6} (DW)^{2.34}$$

$$r = 0.95.$$

WT is given in kg, DW in mm.

The largest specimen in the sample, a female, was one of the largest "tortillas" ever seen. There are no data on size at birth, as no embryos were found. Lack of knowledge of the size of the young of the year also prevented insight on size segregation. Term-embryos in *M. rochebrunei*, a closely related, similar sized species from west Africa, were 340–350 mm wide (Cadenat 1960). Since *Mobula* at birth has a DW of about 1/3 of the adult, size at birth would be about 350 mm DW. This information argues in favor of size segregation in *M. munkiana*. Male to female ratio was 0.71 ($N = 24$), insignificantly different from 1 (χ^2 test $P > 0.05$). Both sexes were caught in the same net sets, indicating that males and females school together, and that there was no sex segregation, either geographic or behavioral.

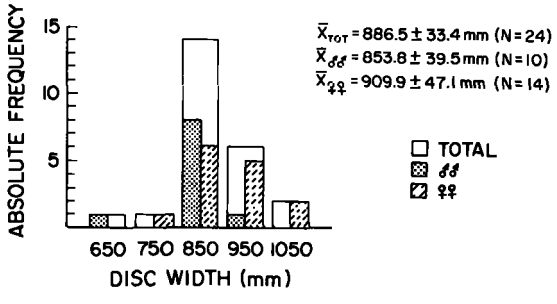

FIGURE 10.—Size-frequency distributions of *Mobula munkiana* (means ±2 SE).

A dried, twisted male carcass, for which morphometrics could not be obtained, with a calculated DW of 895 mm, had long, well-developed claspers, markedly protruding beyond the pelvic fins. Based on other mobulid species, this condition indicates sexual maturity. A second specimen, with a disc 686 mm wide, had small and pliable claspers, and the ratio between clasper length and pelvic fin length, both measured from tip to anterior margin of vent, was 0.88. At this ratio, both *M. thurstoni* and *M. japanica* are immature. Two *M. munkiana*, 871 and 872 mm DW, differed greatly in the relative size of their claspers: one possessed slightly longer claspers than the pelvic fins (ratio = 1.10), and an incipient hardening of the cartilage was apparent; in the other specimen the claspers were much shorter than the pelvics (ratio = 0.84), and still soft. This information suggested that male sexual maturity in *M. munkiana* began at about 870 mm DW.

The largest female specimen was sexually mature, as it had a large, flaccid left uterus, and the enlarged left ovary consisted mainly of about 30 macroscopic ova (size range 2–15.2 mm).

Ten stomachs were examined: four were empty, three contained unidentifiable whitish matter, and three were full of planktonic crustaceans. A list of prey species ranked by decreasing %IRI is given in Table 6. *Mysidium* sp. appeared to be the main staple of *M. munkiana*'s diet. *Mobula munkiana* is thus similar to the wintering young of *M. thurstoni*. One of the stomachs contained coarse coral fragments and small gastropod shells, perhaps ingested by the ray while foraging on mysids near a sandy substrate. The west African species *M. rochebrunei* appeared to have similar feeding habits, as Cadenat (1960) found mysids and a few larger postlarval stomatopods in the stomachs of several specimens.

I have no record of remoras associating with *M. munkiana*. The only parasitic crustacean

found was *Pupulina* cf. *minor* (Copepoda: Caligidae) from the skin.

Among *M. munkiana*'s distinguishing features are its neritic preferences combined with its social habits. This is the only mobulid species in the Gulf of California that was consistently seen in schools. It is not known whether this is a seasonal behavior, or a permanent ethological feature of the species. Schools appear as a conspicuous dark patch, sometimes a few tens of meters in diameter, as they slowly cruise along the coastline in shallow water. The presence of the school is often also highlighted by the frequent, simultaneously leaping individuals, which betray its position from a long distance. Similar behavioral traits (schooling and leaping) have been reported for two closely related species from the Atlantic, *M. hypostoma* (Bancroft 1829; Coles 1910, 1916a) and *M. rochebrunei* (Cadenat 1960). During leaps, *M. munkiana* occasionally reached a height of about two DWs. Two types of leaps were observed: rising vertically head first and landing flat with the belly on the sea surface with a loud clap (breach), and spinning one to three times around the main transverse body axis (somersault).

A salient feature of *M. munkiana*'s ecology in this area is its winter occurrence when all other mobulids are absent or at their lowest numbers. *Mobula munkiana* apparently subsists then chiefly on the mysid shrimp, *Mysidium* sp., which is also the main food for young wintering *M. thurstoni*. However, *M. munkiana* frequents the area occasionally in summer: two specimens were caught by surface gill net in Bahia de la Ventana in July 1983. Even during the season in which it is most abundant, *M. munkiana* is seen in "pulses", as its occurrence at any particular location is spotty. It may occur in large numbers at one location for a few days, and then be absent for 1 or 2 weeks. This observation suggests the possibility that *M. munkiana* lives in large concentrations, perhaps composed by several schools, which travel along the coast. A similar phenomenon was observed off the Senegal coast by Cadenat (1960) in *M. rochebrunei*, a species which is closely related to *M. munkiana* both morphologically and ecologically.

It is conceivable that mobulids in the northern half of the eastern tropical Pacific mate and give birth in summer, based on the few term and near-term embryos found in summer in *M. thurstoni* and *M. japanica*, and from anatomical evidence of mating activity in adult males *M. thurstoni* and *M. japanica*. That such a hypothesis can also be extended to *M. munkiana* is supported by lack of reproductive activity in any of the specimens collected during the fall or winter, and that newborn and young-of-the-year are missing from the sample. This evidence corroborates the hypothesis that the local waters are a wintering ground for *M. munkiana*, which then migrates into an unknown area (perhaps the northern Gulf of California) during the warmer season for mating and pupping.

The possible causes of this ecological difference between *M. munkiana* and the other mobulids are many, and open to speculation. Mysid abundance may be declining in summer in the southern Gulf of California, and *M. munkiana* perhaps migrates to areas where this crustacean or related species abound during the warmer season. Alternatively, *M. munkiana* could be excluded from this region in spring by competition with the incoming, larger *M. japanica* and adult *M. thurstoni*. Finally, *M. munkiana* may be moving during the summer into an area which is more suitable for its reproductive needs. Unfortunately, this recently discovered species is very little known, and it has been reported only from the Gulf of California and Ecuador, although its distribution probably extends to other coastal areas of the tropical east Pacific (Notarbartolo-di-Sciara 1987).

TABLE 6.—Prey species found in three stomachs of *Mobula munkiana* ranked by decreasing Index or Relative Importance (symbols as in Table 2). Identifiable copepod species included *Undinula vulgaris*, *Rhincalanus nasutus*, and *Scolecithrix danae*. The stomatopods found were "erhithrus" larvae. One unidentified food item was a fragment of a larger crustacean, probably an euphausiid.

Prey species	*N*	%*N*	*M*	%*M*	%*F*	IRI	%IRI
Mysidium sp.	293.40	97.80	287.40	95.80	100.00	19,360	97.84
Stomatopod larvae	4.65	1.55	9.06	3.02	66.67	304	1.54
Copepoda	1.59	0.53	1.44	0.48	66.67	67.3	0.34
Other	0.37	0.12	2.10	0.70	66.67	54.7	0.28

Mobula tarapacana (Philippi 1892) Local name: vaquetilla

Mobula tarapacana is not a common species in the study area. Seven specimens were collected, one of which, a premature male embryo, was expelled by a large female while she was being landed. Of the postnatal individuals, two were male (DW range 2,476–2,494 mm), and four were female (2,704–3,052 mm). All were caught in Bahia de la Ventana between 9 June and 30 October 1983. All but two of the specimens were weighed. The following equation describes the WT/DW relationship for *M. tarapacana* (where WT is given in kg, DW in mm):

$$WT = 2.378 \times 10^{-8}(DW)^{2.92}$$

$$r = 0.998.$$

Although all sampled postnatal *M. tarapacana* were large, smaller individuals are known from the area, as can be seen in photographs taken at Punta Arena de la Ventana in summer 1981 (courtesy Felipe Galvan Magaña, CICIMAR, La Paz, Mexico; also Greg B. Deets[3]). This information argues against geographical size segregation of *M. tarapacana*. Data on the embryo provide no indication of size at birth, since it was still far from term. Pale pigmentation was apparent only around the head and pelvic regions, and the external yolk sac was present (Fig. 5B). The embryo, expelled tail first, was alive at birth. Judging by its size it had filled the left uterus completely and must have been the sole developing embryo.

The small size of the sample does not permit any clear inference on size at sexual maturity for *M. tarapacana*. Some indication, however, can be obtained by comparison with similar species. Of the two postnatal males, the specimen with a disc 2,476 mm wide appeared to be immature: no seminal fluid was found in the ducti deferentes, the testes were small and apparently little developed, and the ratio between clasper length and pelvic fin length was 0.94. Conversely, the second postnatal male, with a disc of approximately the same width (2,494 mm), possessed claspers longer than pelvics (ratio = 1.14), and the testes were well developed. Thus, sexual maturity in male *M. tarapacana* begins around a DW of 2,400–2,500 mm. The specimen with a DW of 2,704 mm, one of two nonpregnant females, had a bulky left ovary, containing numerous large eggs; the largest, 32 mm in diameter, weighed 12 g. Similar features appeared to be associated with sexual maturity in female *M. thurstoni* and *M. japanica*. The left ovary of another specimen, DW 2,831 mm, was smaller, and the diameter of the largest ovum was 18.6 mm, indicating that a DW of 2,700–2,800 mm denotes a transitional stage for female *M. tarapacana*, in which both mature and nonmature individuals can occur.

Twelve echeneidids were recovered from *M. tarapacana*. Three were *Remora remora* (size range: 108–229 mm SL), and nine were *R. albescens* (74–159 mm SL). The following crustacean parasites were also found: one cymothoid isopod (still in an unidentifiable aegathoid stage) and *Pupulina flores* (Copepoda: Caligidae) on the skin, *Entepherus laminipes* (Copepoda: Cecropidae) on the branchial filter plates, and *Eudactylina* sp. (Copepoda: Eudactylinae) in the gills.

Mobula tarapacana is strictly a summer and fall visitor to this region (Fig. 6C). This species is often found farther from the coast than *M. thurstoni* and *M. japanica*, and may have more pelagic habits. Four of the five stomachs examined (all from specimens caught in summer) were almost empty. Only traces of food were found among the folds of the stomach epithelium. Prey included four species of copepods (*Acartia* sp., *Pontella* sp., *Temora discaudata*, and *Undinula vulgaris*), hiperiid amphipods, one brachiuran (family Calappidae), one euphausiid, two caridean decapods (one of which belonged to the family Alpheidae), megalopa and stomatopod larvae, and a fish egg. The fifth stomach, from a late October capture, contained the remains of 27 fishes (probably carangids 15–30 cm long, and a smaller anchovy-like species). Small tetraodontids had been found before in the stomach of a *M. tarapacana* caught in Bahia de la Ventana (Felipe Galvan Magaña[4]). On this basis it is impossible to determine whether *M. tarapacana* is a specialized ichthyophagous ray, with the few crustacean items accidentally ingested while swimming, or a generalized feeder. The mesh size of this species' branchial filter plates is indeed greater than in other *Mobula* species (Notarbartolo-di-Sciara 1987). However, filter-

[3]Greg B. Deets, Long Beach State University, CA, pers. commun. 1984.

[4]Felipe Galvan Magaña, CICIMAR, La Paz, Mexico, pers. commun. 1983.

feeding on planktonic crustacea still appears to be a feasible foraging technique for *M. tarapacana*, judging from the size of its branchial sieve as it compares with the average-sized crustacean prey.

SUMMARY AND CONCLUSIONS

Four species of *Mobula* were found in the southern Gulf of California. The most abundant species, *M. thurstoni*, was present year-round, but only the smaller individuals were seen during the winter. The bulk of the population, including the adults, appeared in early spring. Numbers began declining in July. *Mobula japanica*, the second most abundant species, was comprised of only large individuals; numbers progressively increased from March throughout July. Large *M. japanica* were rare in winter, but were occasionally caught then. *Mobula tarapacana* is the rarest mobulid in the area, yet its presence as a summer and fall visitor is well known and predictable; it is believed by the local fishermen to be more abundant farther offshore. All three species share a similar pattern of peak summer seasonal abundance. The reverse is true for *Mobula munkiana*, it being most abundant in winter, and almost totally absent during the rest of the year. It is not known where any species goes when not seen in the area. Seasonal migrations within the epipelagic habitat to different areas of the Panamic region are likely, but unverifiable because of the present lack of knowledge of the occurrence of identified *Mobula* species south of the Gulf of California. Alternatively, devil rays may spend part of the year in midwater, or near the sea bottom, therefore disappearing from sight and reach.

There is a striking similarity between the array of mobulid species found in the Gulf of California (and probably along the Pacific coast of tropical America) and the mobulid fauna from the tropical waters off west Africa. The family is represented in both areas by *Manta birostris* and by four species of *Mobula*: *M. thurstoni*; *M. japanica* (reported from west Africa as *M. rancureli* by Cadenat 1959); *M. tarapacana* (reported as *M. coilloti* for African waters by Cadenat and Rancurel 1960 and Stehmann 1981); and a small gregarious form, represented in the Gulf of California by *M. munkiana* and off west Africa by the closely related *M. rochebrunei* (Notarbartolo-di-Sciara 1987). Tropical coastal areas off west America and west Africa are known to be among the most productive tropical waters in the world, because of comparable large-scale atmospheric and oceanographic circulation patterns (Sverdrup et al. 1942). It is conceivable that the ecological similarity between these two regions is reflected in similar faunal associations, especially as far as low levels of the tropic chain (e.g., plankton-feeding vertebrates) are concerned.

The Gulf of California presents a unique environment in the eastern Pacific Ocean, with extreme annual water temperature ranges, wind-induced mixing and upwellings, and subsequent great productivity (Roden 1964; Brusca 1980). Upwelling is caused along the peninsular coast by the southerly winds prevailing during the warmer months. This environment apparently creates optimal conditions for the existence of the euphausiid shrimp *Nyctiphanes simplex*, which is found in great abundance in the neritic habitat between spring and midsummer, before the intense August heat causes a decline in its numbers (Brinton and Townsend 1980). The following data are combined in Figure 6 to provide an overview of the possible relationship between the seasonality of predator and prey in the study area: a) the relative importance of *Nyctiphanes simplex* and *Mysidium* sp. in the diet of *M. thurstoni*; b) the relative abundance of *N. simplex*; the occurrence of *M. tarapacana* (c) and *M. munkiana* (d) in the catch; and the relative abundances of *M. japanica* (e) and *M. thurstoni* (f) (no data on the biology of *Mysidium* sp. are available).

Young *M. thurstoni* and all *M. munkiana* examined in winter appeared to subsist largely on *Mysidium* sp., whereas adult *M. thurstoni* and *M. japanica* caught during the warmer months fed exclusively on *N. simplex*. An extreme degree of feeding specialization was evident in all mobulid species in which quantitative analyses of the stomach contents was possible; most prey forms, other than *N. simplex* and *Mysidium* sp., were so rare that they were probably ingested accidentally. Stenophagy was linked to feeding specialization in another myliobatiform species, the mollusk-feeder *Rhinoptera bonasus* (Schwartz 1966; Smith and Merriner 1985). These results suggest that devil rays are highly efficient in locating and selecting their preferred food. They may be aided during this behavior by their prey's habit of swarming. Competitive interaction is to be expected between sympatric species-pairs which are closely related both taxonomically and ecologically. Food-resource partitioning is known to occur in sympatric species-pairs of skates

(McEachran et al. 1976). This condition, however, is not necessarily true when the sought-after resources are not in short supply (Zaret and Rand 1971). This may be the case of *M. thurstoni* and *M. japanica* feeding together on *N. simplex* when the abundance of euphausiids is at its peak. Competition should occur, however, in late summer, when prey numbers decline. It would be interesting to determine whether the slight morphological and behavioral differences between potentially competing species pairs (*M. thurstoni*/*M. munkiana* in winter, *M. thurstoni*/*M. japanica* in spring and summer) influence or reflect partitioning of their habitat when food resources become limiting, as was described for both freshwater (Werner and Hall 1977) and marine teleosts (Hixon 1980; Larson 1980).

This overview of the ecology and natural history of mobulids in the Gulf of California is based on field investigations made chiefly in 1983, a year in which the El Niño perturbation was particularly severe (Cane 1983). Although in terms of fishermen's experience the year 1983 was not unduly different, as far as mobulid relative abundance and seasonality are concerned, the abnormally high water temperatures resulting from El Niño may have affected the devil rays studied in subtle ways; therefore this investigation should be repeated in a normal year.

According to the fishermen, the abundance of sharks (mostly carcharhinids and sphyrnids) on which their activity is based is declining. This decline will probably result in an increase of mobulid fishing effort. It is of concern that 72% of the specimens of *M. thurstoni* caught were immature (DW <1,500 mm).

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NOTES ON DECAPOD AND EUPHAUSIID CRUSTACEANS, CONTINENTAL MARGIN, WESTERN ATLANTIC, GEORGES BANK TO WESTERN FLORIDA, USA

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ABSTRACT

Twenty-six species of decapod crustaceans in 16 families and 1 species of euphausiid are reported from the outer continental shelf, submarine canyons, and nearby slope of the eastern and southeastern United States. Station data are given for all collections made with the aid of submersible and surface vessels. Bathymetric and geographic distributions are summarized for six species (*Lithodes maja*, *Munida forceps*, *M. longipes*, *Chacellus filiformis*, *Dissodactylus juvenilis*, *Euchirograpsus americanus*) whose ranges are extended. Comparative descriptive notes are given for other forms that have uncertain identities and need further study (*Alpheus* cf. *amblyonyx*, sp. near *Ligur*, *Munidopsis* cf. *transtridens*).

Records of decapod crustaceans from the outer continental shelf, submarine canyons, and nearby slope off the eastern United States have accumulated in my files to the point that it seems appropriate to publish them with notes on the samples taken in that habitat. Specimens were collected with the aid of deep and shallow water submersibles and surface vessels operated cooperatively by the Lamont-Doherty Geological Laboratory, Columbia University, Palisades, NY, with sponsors listed hereinafter, and between Rutgers University, Center for Coastal and Environmental Studies, and Department of Horticulture and Forestry, New Brunswick, NJ; the Northeast Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, Woods Hole, MA; and the Southeast Fisheries Center Laboratories, NMFS, NOAA, at Panama City, FL, and Pascagoula, MS (Able et al. 1982, 1987; Grimes et al. 1980a, 1986; and Lamont-Doherty records). Vessels (see Table 1) and their sponsoring institutions were DSRV *Alvin*, Woods Hole Oceanographic Institution, Woods Hole, MA; RV *JSL I* and *JSL II*, Harbor Branch Oceanographic Institution, Inc., Fort Pierce, FL; RV *Cape Henlopen*, University of Delaware, Lewes, DE; RV *Eastward*, Duke University, Beaufort, NC; RV *Endeavor*, University of Rhode Island, Kingston, RI; RV *Gyre*, Texas A&M University, Galveston, TX. The specimens have been deposited in the crustacean collection of the United States National Museum of Natural History (USNM).

Bathymetric and geographic distributions of many decapod crustacean species from the North American continental shelf in the western Atlantic were reviewed by Squires (1965), Williams and Wigley (1977), Wenner (1982), and Williams (1984). Wenner and Boesch (1979) and Wenner and Windsor (1979) included a deeper dwelling component in their treatments of epibenthic decapods collected from the continental shelf and slope. Collections by workers from the contributing institutions listed above include 26 species of decapod crustaceans in 16 families, some unidentified fragments, and 1 species of euphausiid listed in Table 1. Named localities are listed from north to south (see Figures 1 and 2); successive visits are arranged chronologically, and species present in each collection are inventoried alphabetically.

Species whose reported bathymetric or geographic ranges are extended by presence in these collections are discussed below. Some of the forms have uncertain identities that may be clarified after more thorough study of samples from the outer shelf-upper slope environment.

SUPERFAMILY ALPHEOIDEA

Family Alpheidae

Alpheus cf. *amblyonyx* Chace 1972. Three lots of specimens key out to *A. amblyonyx* (see Chace 1972), but they differ in several respects from it.

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TABLE 1.—Records of decapod crustaceans from submarine canyons, outer listed from north to south, successive visits are arranged chronologically, and in footnote. * = Bathymetric or geographic range extension.

Locality	Depth (m)	Cruise/ station	Date
---------- Lamont-Doherty ----------			
Lydonia Canyon			
40°21'N, 67°41'W	700-790	Gyre	8 June 1982
40°22'N, 67°41'W	462	Alvin 1269	18 Sept. 1982
40°21.69'N, 67°39.97'W	906	Alvin 1270	19 Sept. 1982
Oceanographer Canyon			
40°23.7'N, 68°07.8'W	415-680	Eastward 35982	15 May 1979
40°16.3'N, 68°07.2'W	660-1,424	Eastward 35991	19 May 1979
Slope Area III between Hydrographer and Veatch Canyons			
39°50'N, 69°25'W	500-2,000	Endeavor	21 Oct. 1981
Slope Area II between Toms and Meys Canyons			
39°13.05'N, 72°30.93'W	174	JSL I 1081	1 Aug. 1981
39°12.64'N, 72°30.87'W	200	JSL I 1081	1 Aug. 1981
39°11.06'N, 72°33.66'W	219	JSL I 1082	1 Aug. 1981
Hendrickson Canyon			
39°03.52'N, 72°28.45'W	1,420-1,425	Alvin 1118	19 July 1981
Baltimore Canyon			
38°09.6'N, 73°49.2'W	155-160	Eastward 35940	2 May 1979
38°07.9'N, 73°48.8'W	185-190	Eastward 35938	2 May 1979
38°08.5'N, 73°49.9'W	280-570	Eastward 35944	2 May 1979
38°09.6'N, 73°49.2'W	155-160	Eastward 35940	2 May 1979
38°08.7'N, 73°49.3'W	148-174	Eastward 35939	2 May 1979
38°11.7'N, 73°52.8'W	150-245	Eastward 35942	2 May 1979
38°03.6'N, 73°46.2'W	910-925	Eastward 35946	3 May 1979
38°07.6'N, 73°46.8'W	152-163	Eastward 35947	3 May 1979
38°06'N, 73°50'W	200-800	Eastward 35979	7 May 1979
38°04.93'N, 73°47.79'W	1,024	Alvin 1109	11 July 1979
38°08'N, 73°50.7'W	600-700	B10-1	28 May 1981
34°04'N, 73°46'W	1,000-1,200	Cape Henlopen CM02	13 June 1981
38°09'N, 73°51'W	171-381	JSL I 1083	2 Aug. 1981
38°09.99'N, 73°51.86'W	381	JSL I 1083	2 Aug. 1981
38°11'N, 73°51'W	165	JSL I 1088	4 Aug. 1981
38°11'N, 73°51'W	165-244	JSL I 1088	4 Aug. 1981
38°10.1'N, 73°52.2'W	225	JSL I 1084	4 Aug. 1981

continental shelf and upper slope off the eastern United States. Named localities are species inventoried in each collection are listed alphabetically. Family abbreviations

Species	*N*, Sex	Notes, family[1]
	---------- Lamont-Doherty ----------	
Munida valida Smith	1♂	Dredge, Ga
Pagurus politus (Smith)	1♂	Pag
**Munidopsis* cf. *transtridens* Pequegnat and Pequegnat	1♂	Ga
Pandalus propinquus G. O. Sars	1♀	Pan
Panadalus propinquus	1♂, 3♀	Day dredge, Pan
Metacrangon jacqueti agassizii (Smith)	1♂	Dredge, Cr
Nematocarcinus ensifer (Smith)	1 spec.	Camera, N
Euprognatha rastellifera Stimpson	1♀ ovig.	M
**Euchirograpsus americanus*	1♀	Gr
Eumunida picta Smith	1♀	Ch
Munida iris iris A. Milne Edwards	1♂ (parasitized)	Ga
**Munidopsis* cf. *transtridens*	1♂	Ga
Cancer borealis Stimpson	1 juv.	Can
**Euchirograpsus americanus* A. Milne Edwards	1♂, 3♀	Gr
Euprognatha rastellifera	1♂	Day dredge, M
Cancer borealis	1♀	Day dredge, Ca
Euprognatha rastellifera	1♂	Day dredge, M
**Munida longipes* A. Milne Edwards	1♂, 2♀ ovig.	Day dredge, Ga
Pagurus politus (Smith)	1♀	Day dredge, Pa
**Chacellus filiformis* Guinot	1♂	Day dredge, Go
Euprognatha rastellifera	1♂	Day dredge, M
Munida iris iris	3♂, 3♀	Day dredge, Ga
Plesionika edwardsii (Brandt)	1♀ ovig.	Day dredge, Pan
Cancer borealis	2 juv.	Day dredge, Ca
Cancer irroratus Say	1♂	Day dredge, Ca
Euprognatha rastellifera	1♂	Day dredge, M
Cancer borealis	1♂	Day dredge, Ca
Sergestes arcticus	1♀	Day dredge, S
Collodes robustus Smith	1♀ ovig.	Day dredge, M
Eumunida picta	4 juv., 1♂, 5♀	Camera sled, Ch
Lebbeus polaris (Sabine)	1♀	Camera sled, H
**Munidopsis* cf. *transtridens*	1♂	Airplane wreck, Ga
Sergestes arcticus Kröyer, euphausiid and copepods	9♀	Bongo net, S
Sergestes arcticus	1♀	Bongo net, S
Bathynectes longispina Stimpson	1♂	Po
**Lithodes maja* (Linnaeus)	1♀	L
Cancer irroratus	1♂	Ca
Munida iris iris	1♂	Ga
Munida iris iris	1♂	Ga
Pagurus politus	1♂	Pag

TABLE 1.—*Continued.*

Locality	Depth (m)	Cruise/ station	Date
38°09.51'N, 73°51.25'W	338	JSL I 1089	5 Aug. 1981
38°11'N, 73°51'W	402	JSL I 1090	5 Aug. 1981
38°02'N, 73°45'W	200-1,400	Gyre	26 May 1982
Norfolk Canyon			
37°03'N, 74°37'W	215	JSL I 1093	7 Aug. 1981
---------- Rutgers ----------			
Lydonia Canyon			
40°27.25'N, 67°42.30'W	160-178	JSL I 1070	23 July 1981
Veatch Canyon			
40°03'20"N, 69°45'23"W	124-126	JSL I 1074	25 July 1981
40°03'00"N, 69°45'25"W	123-128	JSL I 1075	26 July 1981
39°59'51"N, 69°35'00"W	213-244	JSL I 1076	26 July 1981
40°00.91'N, 70°50.79'W	243-304	JSL II 901	29 July 1984
40°01.29'N, 70°50.63'W			
40°03.24'N, 71°05.01'W	193-209	JSL II 902	29 July 1984
40°02.96'N, 70°20.84'W	181-195	JSL II 909	2 Aug. 1984
40°12.73'N, 70°19.77'W	103-104	JSL II 910	2 Aug. 1984
40°12.51'N, 70°20.22'W	103-104	JSL II 910	2 Aug. 1984
40°02.79'N, 70°11.95'W	183-337	JSL II 911	3 Aug. 1984
40°03.23'N, 70°12.01'W	213-327	JSL II 912	3 Aug. 1984
Off eastern Florida			
28°43'N, 80°02'W	137	JSL I 1565	1 Oct. 1984
28°42.5'N, 80°02.8'W	98-114	JSL I 1566	2 Oct. 1984
Off western Florida			
27°51.2'N, 84°53.7'W	250-260	JSL I 1673	24 Sept. 1985
27°56.2'N, 84°43.9'W	167-175	JSL I 1676	26 Sept. 1985

[1]A, Alpheidae; Cal, Calappidae; Can, Cancridae; Ch, Chirostylidae; Cr, Crangonidae; Ga, M, Majidae; N, Nematocarcinidae; Pag, Paguridae; Pan, Pandalidae; Pi, Pinnotheridae; Po,

Species	*N.* Sex	Notes, family[1]
Rochinia crassa A. Milne Edwards	1♂	M
Pandalus propinquus	2♀	Pan
Sergestes arcticus	3♂	Camera, S
Bathynectes longispina	1 juv.	Po
---------- Rutgers ----------		
**Munida forceps* A. Milne Edwards	1♂	Bot. t. 11.2°C, Ga
Munida iris iris	1♂, 4♀ ovig.	Bot. t. 11.4°C, Ga
Pagurus politus	1♂	Bot. t. 11.4°C, Pag
Acanthocarpus alexandri Stimpson	2♀	Bot. t. 11.5°C, Ca
**Chacellus filiformis*	3♂ (1 juv.)	Bot. t. 11.2°C, Go
	4♀ (1 juv., 3 ovig.)	Bot. t. 12.2°C, Ga
**Munida forceps*	1♂, 1♀ ovig.	Bot. t. 12.2°C, Ga
Munida iris iris	1♂	
**Alpheus* cf. *amblyonyx* Chace	1♂	H
**Alpheus* cf. *amblyonyx*	1 juv.	H
Munida iris iris	1♂	Ga
**Munida forceps*	1♂	Ga
*Goneplacid? crab		Go
**Chacellus filiformis*	1♂,1♀	Go
**Munida forceps*	2♂	Ga
**Munida forceps*	1♂	Ga
Meganyctiphanes norvegica (M. Sars)	1	E
**Munida forceps*	1 juv., 1♀ ovig.	Ga
**Chacellus filiformis*?	Frag. of chela	Go
Meganyctiphanes novegica	45	E
Meganyctiphanes novegica	2	E
Meganyctiphanes novegica	8	E
Alpheus cf. amblyonyx	2♂, 1♀, 1 juv.	Tilefish burrow, A
Munida forceps	2♀	Tilefish burrow, Ga
Crab (xanthid or goneplacid frags.)	1	Tilefish burrow, Ga
**Alpheus* cf. *amblyonx*	1♀	Tilefish burrow, Ga 12.1°C, A
Munida forceps	1	Tilefish burrow, Ga
*Near *Ligur* Sarato	2♂, 1♀	Tilefish burrow, Hi
**Munida forceps*	1♂, 2♀ ovig. 1 juv.	Tilefish burrow, Ga
**Dissodactylus juvenilis* Bouvier	1♀ ovig.	With *Clypeaster ravenellii* A. Agassiz, 13.8°C, Pi

Galatheidae; Go, Goneplacidae; Gr, Grapsidae; E, Euphausiidae; H, Hippolytidae; L, Lithodidae; Portunidae; S, Sergestidae.

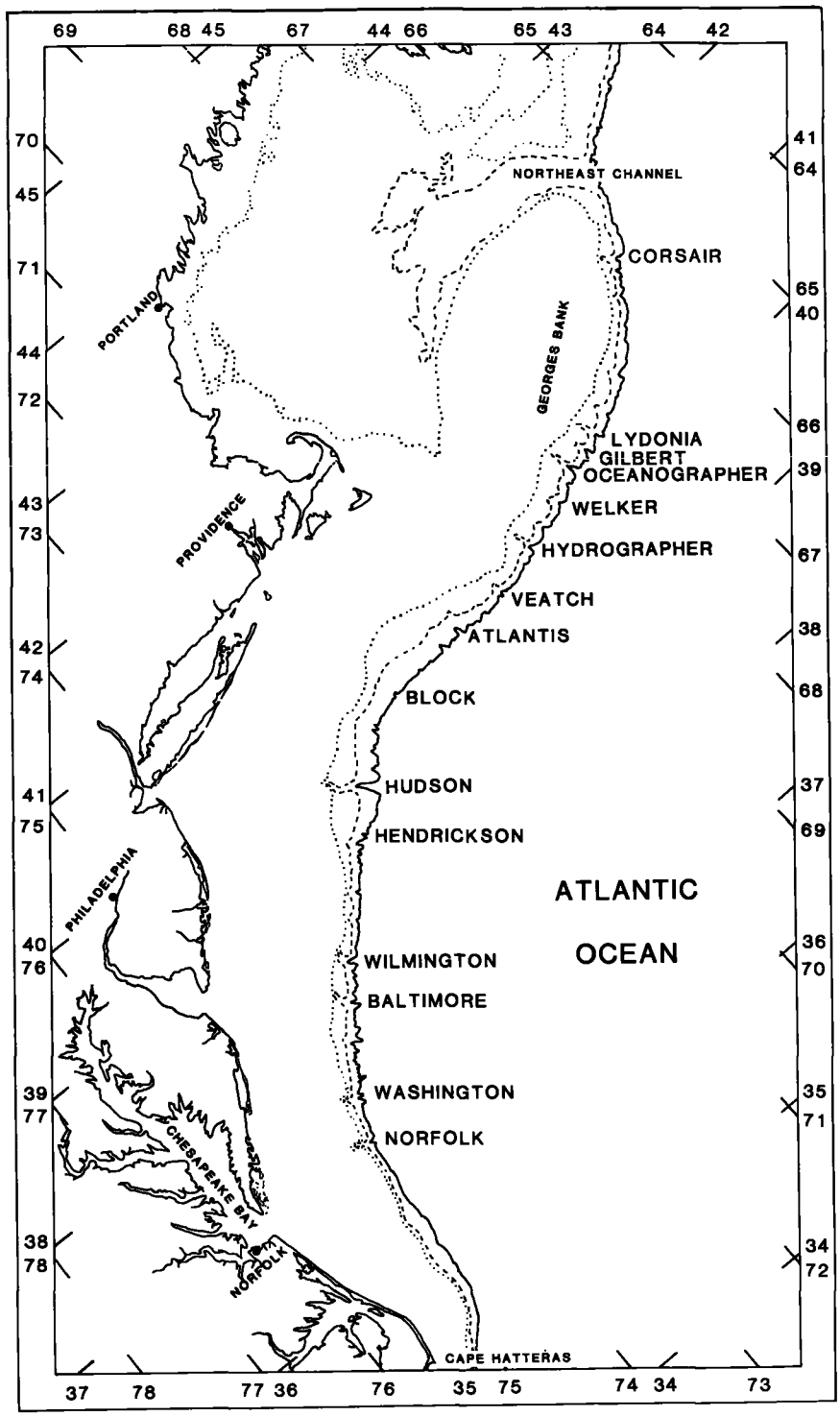

FIGURE 1.—East coast of United States showing continental shelf, slope and submarine canyon areas from which species listed in Table 1 were collected. Base map adapted from Uchupi (1965) and Veatch and Smith (1939). Contours in m: dotted = 100, dashed = 200, solid = 1,000.

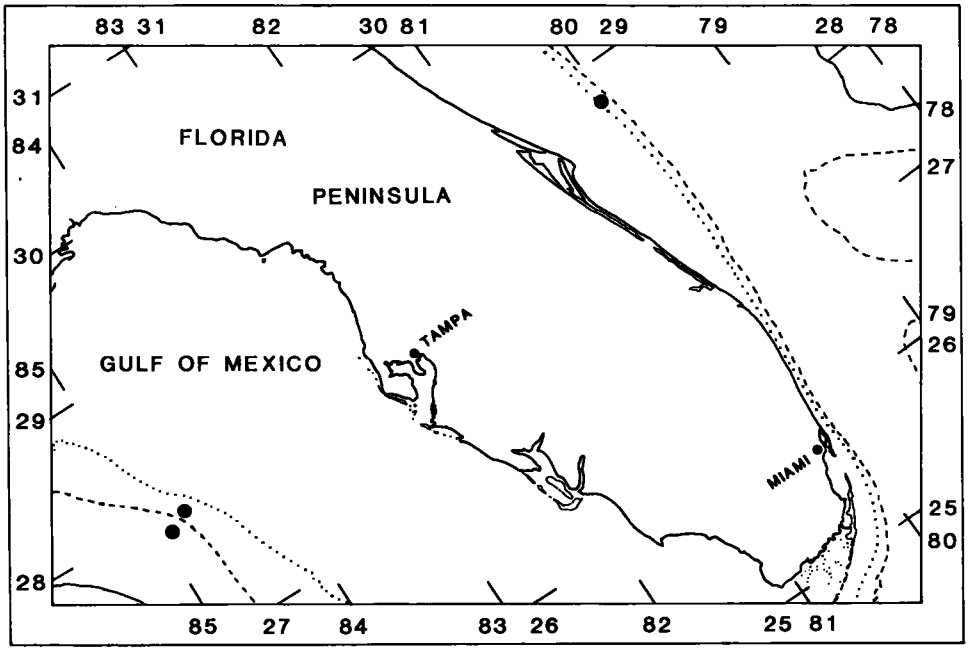

FIGURE 2.—Florida peninsula including continental platform showing slope localities from which species listed in Table 1 were collected. Base map adapted from Uchupi (1965). Contours in m: dotted = 100, dashed = 200, solid = 1,000.

Some of the more obvious differences for the Veatch Canyon material are: Rostrum relatively shorter in relation to basal antennal article. Dorsal spines of telson more distally positioned, anterior pair at about midlength of telson but subject to some variation. Antennal scale with distal spine exceeding antennular peduncle. Major chela of mature male missing, but juvenile with fingers bent mesad; dactyl moderately arched in profile and greatly overreaching fixed finger, somewhat twisted, compressed proximally and dorsally producing thin dorsal margin, external surface somewhat concave, occlusive surface lacking plunger but broadened and strongly calcified distally, fitted to obliquely flattened occlusive surface of fixed finger lacking socket but provided with small stout tooth on mesial surface; palm with obsolescent dorsal and ventral notches.

In the Florida material, the differences are: Chela relatively stout, fingers stout and thick, dactyl opening and closing in oblique plane, tip rounded, bearing short plunger fitting into shallow socket on occlusive surface of fixed finger, latter with 2 short spines on mesial surface; palm with shallow notch on dorsal margin and slight offset on ventral margin, outer surface smooth but base of dactyl flanked by distodorsal groove and longer mesial groove. Second pleopod of male with appendix masculina exceeding appendix interna. Uropodal exopod with lateral margin ending in single sharp tooth and rather long, uncolored movable spine; endopod lacking distal spines but bearing subterminal tuft of setae on dorsal surface.

Alpheus amblyonyx is distributed from Quintana Roo (type locality, Bahía de la Ascensión), Yucatan Peninsula, Mexico, to Puerto Rico, Saint Thomas and Dominica; sublittoral (Chace 1972).

Family Hippolytidae

Three small shrimps, two males and one female from *JSL* 1673 in the Gulf of Mexico off Florida, represent an undescribed species resembling members of the genus *Ligur* Sarato, 1885 from the western Mediterranean and Indo-Pacific region (see Holthuis 1947, 1955). The specimens were associated with burrow systems of the blueline tilefish, *Caulolatilus microps* Goode and Bean.

SUPERFAMILY PAGUROIDEA

Family Lithodidae

Lithodes maja (Linnaeus 1758). Southern limit extended from Sandy Hook, NJ (see Williams 1984) to Baltimore Canyon.

SUPERFAMILY GALATHEOIDEA

Family Galatheidae

Munida forceps A. Milne Edwards 1880. Geographic range extended from south of Norfolk Canyon, 36°43.2'N, 74°38.0'W, 252 m (Wenner 1952), to Veatch and Lydonia Canyons off southern New England, 103-337 m.

The distinctive color pattern of this species was described on 14 October 1981 from specimens preserved in formalin 25 July 1981. Carapace (Fig. 3), salmon color with lavender submesial spots on gastric region and interrupted U-shaped bands of same color in nested series on mesogastric region, posterior to cephalic groove, and arching across posterior and posterolateral parts. Oblique red lines on lateral wall of carapace below suture, most prominent band along anterior edge, continued dorsally anterior to antennal peduncle and ending on lateral side of supraocular spine. Median band of same intensity on epistome and labium. Paler oblique lateral band on basal antennular article. Some flecks of red on merus of chelipeds and cross banding on fingers of some individuals.

Munida longipes A. Milne Edwards 1880. Northern limit extended from off Cape Lookout, NC (Williams 1984) to Baltimore Canyon.

Munidopsis cf. *transtridens* Pequegnat and Pequegnat 1971. *Munidopsis transtridens* is known only from the holotype female taken in the southeastern Gulf of Mexico at 1,280 m. The specimens reported here from Baltimore, Hendrickson, and Lydonia Canyons off New Jersey and southern New England, 906-1,425 m, are all males. They resemble *M. transtridens* but differ from it in rostral characters (both longer and shorter, variably narrower or broader, in degree of lateral convexity) and in having chelae strikingly larger than the slender ones of the holotype. Although these differences may be attributable to sexual dimorphism, provisional identification seems best until more material is available for study.

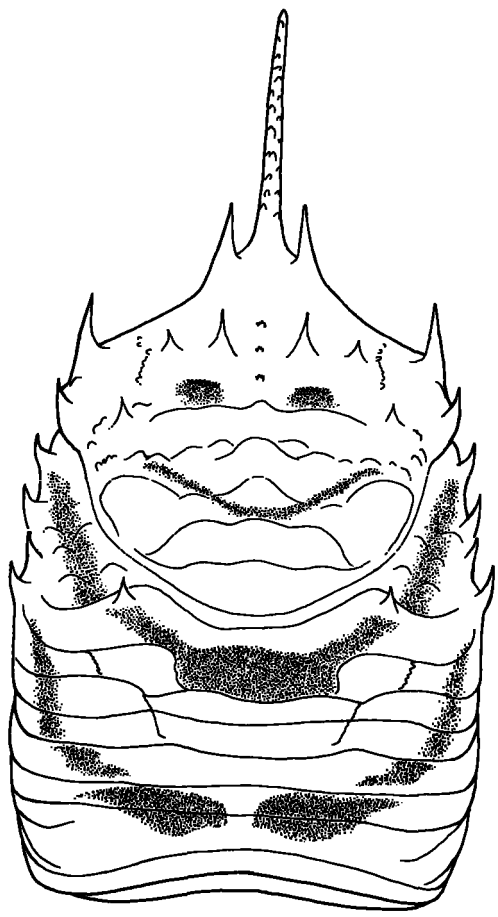

FIGURE 3.—*Munida forceps*, male. Dorsal view of carapace, diagrammatic representation of lavender bands on salmon ground color, carapace length 17.7 mm to base of supraocular spine.

SUPERFAMILY XANTHOIDEA

Family Goneplacidae

Chacellus filiformis Guinot 1969. Geographic range extended from the northern Gulf of Mexico east of the Mississippi River Delta and off the east coast of Florida, 328-400 m (Guinot 1969), to Baltimore and Lydonia Canyons, 160-244 m.

Goneplacid crabs were driven out of secondary burrows in walls of larger burrows constructed by tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, with rotenone. The poison did not kill the crabs but caused them to emerge from the burrow systems enough that they could be collected by

"slurp gun". These burrow systems in Pleistocene clay, referred to by Warme et al. (1978) and Cooper and Uzmann (1980) as "Pueblo Villages", shelter a number of invertebrate and vertebrate species (Able et al. 1982; Bowman 1986; Grimes et al. 1980a, 1980b, 1986). Goneplacids are rare in collections made from surface vessels probably because trawls or grabs cannot efficiently sample the burrow systems in which these crabs have been observed. Galatheids from shallower burrows are more open to capture by conventional means (Churchill B. Grimes[2]).

To the brief color description quoted from Chace by Guinot (1969), the following can be added from notes made 14 October 1981 on mature males, females, and juveniles that were preserved in formalin 25 July 1981, and personal communication from Churchill Grimes (fn. 2). Carapace dorsally spotted with red on off-white background. Same type of spots on pterygostomian, subocular, epistomial, and subbranchial areas, on external maxillipeds, and on merus, carpus, and propodus of chelipeds (dorsally, laterally, and mesially). Spots tending to coalesce along front of carapace and on chelae. Red color more diffuse on dorsal or exposed surfaces of walking legs, becoming more distinct and intense with increasing size. Fingers of chelae black. Dactyls of walking legs white except for darkened tips, but setae pinkish. There is some variation in pattern on individual crabs.

There is variation also in the length of the male first pleopod, both in the USNM series of specimens studied by Guinot (1969) and in the new material reported here. In some specimens of the latter, this appendage exceeds or at least reaches the distal edge of the telson, whereas it is shorter in specimens previously reported from localities further south. In the latter, the third abdominal segment is more angled laterally than in specimens from the north. Thus, there seem to be some differences between the northern and southern populations.

SUPERFAMILY GRAPSIDOIDEA

Family Grapsidae

Euchirograpsus americanus A. Milne Edwards 1880. Geographic range extended north from off Oregon Inlet, NC (Williams 1984) to Oceanographer Canyon at the edge of Georges Bank and nearby continental slope at 155-200 m.

SUPERFAMILY PINNOTHEROIDEA

Family Pinnotheridae

Dissodactylus juvenilis Bouvier 1917. The ovigerous female from the Gulf of Mexico off western Florida, though similar in general features to *D. juvenilis*, is very large for that species. In a recent review of the genus *Dissodactylus*, Griffith (1987) reported *D. juvenilis* from north of Yucatan and the Mississippi Delta. Members of the genus are found in association with clypeastroid echinoids (Schmitt et al. 1973), as was this specimen in a sample that included *Clypeaster ravenellii* A. Agassizi.

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AGE AND GROWTH OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, IN THE NORTHERN GULF OF MEXICO

STANLEY M. WARLEN[1]

ABSTRACT

Experiments on laboratory-spawned and -reared larval gulf menhaden, *Brevoortia patronus*, showed that they formed one otolith growth increment per day and that the increments could be used to estimate their age. Wild larvae from collections in the northern Gulf of Mexico along three transects (Cape San Blas, Florida; Southwest Pass, Louisiana; and Galveston, Texas) were aged. Gompertz growth equations were used to describe the relationship between age and standard length for larvae collected at various locations, and in different seasons and years. MANOVA tests and subsequent pairwise tests were used to test for differences among these growth curves. For the most extensive data set (Southwest Pass, Louisiana), there were significant differences in growth between early season (December) and late season (February) larvae. Early season larvae grew faster than late season larvae. Growth of larvae also differed among December collections and among February collections. The growth model for the pooled data for all wild larvae predicted that they grew from 2.4 mm SL at hatching to 20.4 mm SL at 62 days.

Gulf menhaden, *Brevoortia patronus*, is the most abundant commercial finfish in the Gulf of Mexico and, with 883,500 metric tons (t) landed in 1985 (U.S. National Marine Fisheries Service 1986); it constitutes the largest fishery in the United States. Some aspects of the oceanic early life history of this clupeid are known and are reviewed by Turner (1969), Christmas and Waller (1975), Lewis and Roithmayr (1981), Govoni et al. (1983), and Shaw et al. (1985a). However, virtually nothing is known about the age and growth of the larvae, much less how these parameters vary spatially and temporally. Daily growth increments on otoliths of larval fishes can be used as an indicator of their age, and once the use of this technique, first described by Pannella (1971), is validated for the larvae of an individual species, their ages can be estimated with confidence and growth rates can be determined. Intraspecific growth may be compared for larvae from different areas and seasons (Lough et al. 1982), and from this it may be possible to ascertain how biotic and abiotic environmental variables affect larval growth and survival. The objectives of this study are to 1) validate the periodicity of increment formation in otoliths of larval gulf menhaden, 2) estimate larval growth rates, 3) compare growth rates of larvae from different locations and times, 4) estimate spawning times, and 5) examine possible relationships between larval growth and surface water temperature. This work was part of a larger project designed to investigate the early life history of several economically important fishes and the marine planktonic food webs that support their growth and survival in the northern Gulf of Mexico.

METHODS

Spawning and Larval Rearing

Adult gulf menhaden were collected near Gulf Breeze, FL, and transported to the Beaufort Laboratory, Beaufort, NC (Hettler 1983). After a period of acclimation, adults were induced to spawn in the laboratory. The resultant larvae were used in experiments to validate the periodicity of increment formation on their otoliths and the age at first increment formation.

Beginning February 1983, several thousand newly spawned gulf menhaden eggs were transferred to a tank containing 90 L of filtered seawater. The static water in this tank, kept at 20.5° ± 0.5°C throughout the experiment, was continuously aerated and the salinity maintained at 31 ± 1‰. Photoperiod was 12 hours light:12 hours dark. A food concentration of 25 rotifers (*Brachionus plicatilis*) mL^{-1} was maintained. A green alga, *Nanochloris* sp., was added periodically as food for the rotifers and to aid in removing toxic metabolites. The otoliths of larvae sam-

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pled at 10-, 17-, 24-, and 31-d posthatch were examined.

In January 1984 additional larvae were reared to compliment results of the earlier experiment. Smaller tanks with 60 larvae in 10 L of filtered water were used. Experimental conditions were the same as for the first experiment. The otoliths of larvae sampled at 7-, 14-, and 20-d posthatch were examined.

Larval Collections

Larval gulf menhaden were collected in the northern Gulf of Mexico during six cruises of the RV *Oregon II*. Sampling stations (Fig. 1) along transects LA (off Louisiana) and FL (off Florida) were occupied during 11–19 December 1979, 5–15 February 1980, and 2–12 December 1980 and along transects LA, FL, and TX (off Texas) during 9–24 February 1981, 2–13 December 1981, and 4–16 February 1982. Transect LA is near the Mississippi River outflow off Southwest Pass, LA; transect FL is southwest of Cape San Blas, FL; and transect TX is located off Galveston Bay, TX. Sampling stations were in water depths of 18, 91, and 183 m except off Texas where only the 18 and 91 m depths were sampled.

A multiple opening-closing net and environmental sensing system (MOCNESS) as described by Wiebe et al. (1976) were the primary sampling gear used to capture larvae. Additional samples were taken in oblique tows with a 60 cm bongo frame also fitted with 505 μm mesh nets. Samples were collected day and night and were preserved in 95% ethanol (final concentration ≈75%) within 5 minutes of collection. The ethanol was changed in all samples at least once after initial preservation to prevent dissolution of otoliths in fish from any samples that may have been inadequately preserved. Data from larvae collected at all stations within a transect were combined for that transect.

Estimating Age and Growth

All gulf menhaden larvae were measured to the nearest 0.1 mm standard length (SL). The largest otolith pair (sagittae) was teased from the surrounding tissue, cleaned in distilled water, and then placed on a glass microslide under a thin layer of Flo-Texx[2] mounting medium.

Otoliths were viewed with a compound microscope fitted with a television camera. Growth increments were counted from otolith images on a video monitor at magnifications of at least 400×. An increment appeared as a light, wide incremental band and a dark, narrow, discontinuous band (Tanaka et al. 1981). Increments were generally clearly discernable and easily counted (Fig. 2). Estimated age was the number of increments counted plus an empirically derived value for the

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

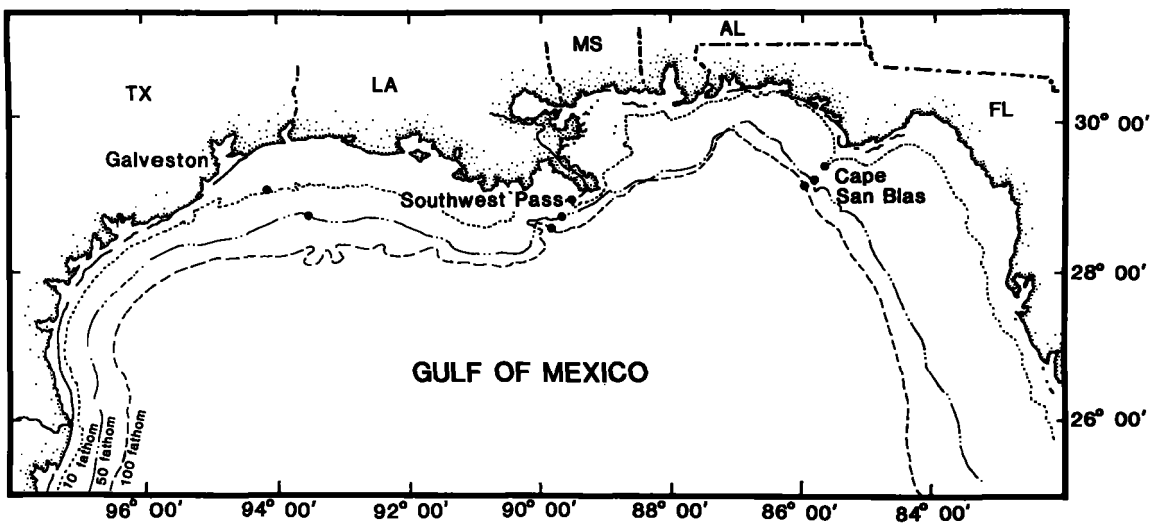

FIGURE 1.—Location of sampling sites from which larval gulf menhaden were collected during cruises of the RV *Oregon II* in December 1979–81 and February 1980–82.

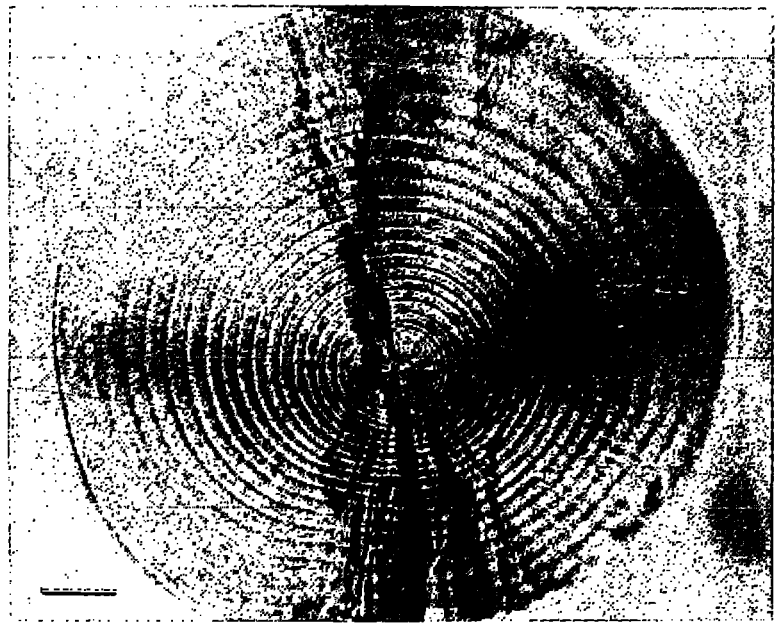

FIGURE 2.—Photomicrograph of a saggital otolith with 22 increments from a 17.4 mm SL field collected larval gulf menhaden. Scale bar represents 10 μm. Growth increments appear as pairs of wide incremental and narrow discontinuous bands.

number of days from spawning to first increment formation. Results of the laboratory experiments established the periodicity of otolith increment formation.

A spawning date was assigned each ageable larva by using the estimated age of the fish in days to back-calculate from the date of capture. It was assumed that there were no differences in either the age at initial increment deposition or the otolith increment deposition rate between locations and seasons and that the rate was not a function of temperature, food, or photoperiod.

Average growth of larvae was described by the Laird version (Laird et al. 1965) of the Gompertz growth equation (Zweifel and Lasker 1976) fitted to estimated age and size at time of capture for fish from all cruises and transects. To stabilize the variance of length over the observed age interval, length data were log-transformed and model parameters were estimated from the log-transformed version of the growth equation. The model was fit to data for each transect within each cruise and for pooled data from all cruises.

Potential differences in the overall growth curves among years and between seasons for larvae caught off Louisiana and between years (1981 and 1982) for larvae caught off Louisiana and Texas were examined by treating the parameters of the Gompertz equation as dependent variables in two-way multivariate analysis of variance (MANOVA) designs. A one-way MANOVA design was used to test for differences among transects (LA, FL, TX) within one season (February 1982). Following significant MANOVA results, prespecified pairwise Hotelling's T^2 test comparisons (Bernard 1981, as modified by Hoenig and Hanumara 1983) were made using the Bonferroni procedure (Harris 1975) to provide conservative tests of statistical significance. Bonferroni critical values for these individual tests were equal to the overall error rate (significance level = 0.05) divided by the number of possible comparisons in the particular MANOVA design. The emphasis in the comparisons was to look for overall differences in the growth of larvae using these statistics as a guide and not to look for differences in individual parameters of the growth models.

Hotelling's T^2 test and MANOVA both require that the data fit a multivariate normal distribution and that the variance-covariance matrices of the populations are not different (Harris 1975). These assumptions are difficult to test and are almost certainly not valid for real data sets (par-

ticularly field data), but they may be nearly valid for many sets of data (Harris 1975). No direct test of normality in a trivariate, joint probability distribution is available (Bernard 1981), but bias arising from nonnormal, multivariate, joint distributions is minimized with large sample sizes (Bernard 1981). While methods are available to test the hypothesis of equal variance-covariance matrices (e.g., Box's modification of Bartlett's test), these methods are very sensitive and even minor differences between group dispersions will likely be discovered (Pimentel 1979). In any event, the use of MANOVA in this paper relies on variance-covariance matrices estimated from nonlinear regressions, and these are not amenable to testing. However, both MANOVA and Hotelling's tests are extremely robust even under violation of the assumptions of homoscedasticity and multivariate normality (Harris 1975).

RESULTS

Increment Formation

The age of gulf menhaden at formation of the first otolith growth increment was estimated from laboratory-reared larvae. The intercept (2.6 days) of the regression of the number of growth increments on known posthatch age of 36 larval gulf menhaden (Fig. 3) was used to estimate posthatch age at formation of the first increment. This value was added to the time from spawning to hatching which at 20°C is 2 days (Powell[3]). This sum (4.6 days) is the estimated time from spawning to formation of the first increment. Hence, it was necessary to add 5 days to each increment count to estimate the age of larval gulf menhaden from spawning.

The periodicity of increment formation was ascertained from the regression of the number of growth increments on the known age (Fig. 3). The slope did not differ significantly (t-test, $P < 0.05$) from 1.0, and thus, on the average, one otolith growth increment was formed per day in laboratory-reared larvae up to 31 days after hatching. Results of a second experiment (Table 1) confirmed this periodicity. The age of gulf menhaden larvae estimated from otolith increment counts (+5) closely approximated the known ages of 51 laboratory-reared larvae. Mean estimated age of larvae differed by <1 day from the known

[3]A. B. Powell, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516-9722, pers. commun. February 1986.

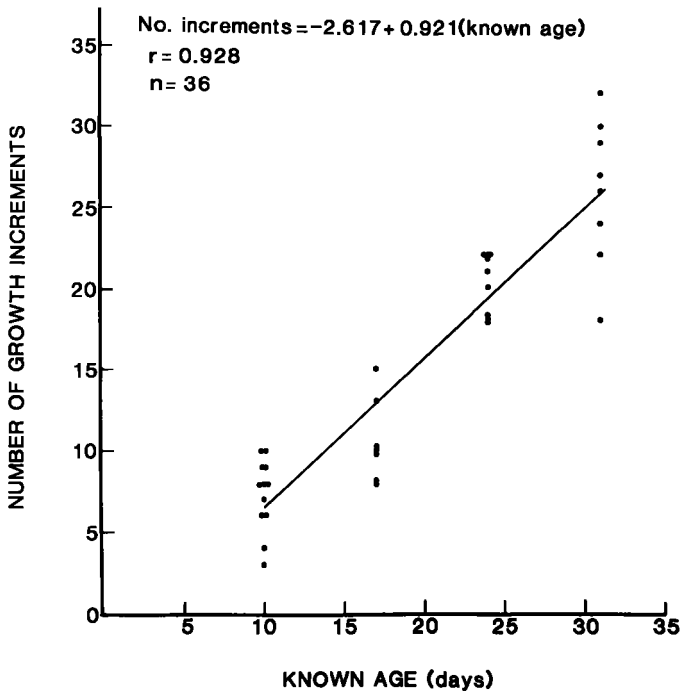

FIGURE 3.—Regression of the number of growth increments on the known posthatch age of 36 laboratory-reared gulf menhaden. Standard error of the slope is 0.108.

TABLE 1.—Standard length (mm) and estimated age (number of otolith growth increments +5) of laboratory-reared larval gulf menhaden. Values in parentheses are 95% interval estimates.

Known age (days)	Number of fish	Mean estimated age	Mean SL
7	13	7.8 (±0.38)	4.7 (±0.28)
14	16	13.2 (±1.14)	6.4 (±0.38)
20	22	19.3 (±0.77)	8.0 (±0.42)

ages and the 95% confidence intervals included the known age in each of the three groups. Some of the variation in the number of growth increments observed in known age larvae (Fig. 3, Table 1) may have been due to 1) poor growing conditions during rearing that could have resulted in reduced growth in underfed larvae, 2) variation in the inception of increment formation as has been observed in other species (Laroche et al. 1983; Fives et al. 1986), and 3) faintness of growth increments in some larvae. In contrast, increments on otoliths of field collected larvae (Fig. 2) were usually very regular and distinct and were more easily observed than those on otoliths of laboratory-reared larvae. I assumed that the growth increment deposition rate was also daily in wild larvae examined in this study.

Age and Growth of Larvae

Average growth of larval gulf menhaden during their first two months of life was described by the Gompertz growth model for pooled length at age data for 2,003 fish representing collections from all six RV *Oregon II* cruises (Table 2, Fig. 4). Larvae ranged in age from 5 to 62 days ($\bar{x}$=24.4 days) and in SL from 3.4 to 28.0 mm ($\bar{x}$=12.6 mm). In the log-transformed model, age accounted for 82% of the variation in length. Gulf menhaden were predicted to have grown from 2.4 mm SL at hatching to 20.4 mm at age 62 days. The size at hatching estimated from the Gompertz equation was only slightly less than the hatching size, 2.6–3.0 mm SL, observed in the laboratory (Hettler 1984). Age-specific growth rates declined from ≈7%/day at age 10 days to <0.4%/day at age 60 days. Maximum absolute growth rate occurred when gulf menhaden larvae were 7.9 mm SL and 13 days old.

The asymptotic length of larvae (21.5 mm SL), determined from the variables of the growth equation, is approximately the size when larvae begin to transform into juveniles. This transformation, described by Lewis et al. (1972) for the closely related Atlantic menhaden, *B. tyrannus*, apparently ends when the fish reach 28–30 mm SL (Suttkus 1956).

In all instances except one transect (TX December 1981, where there was no convergence in the parameter values in the computer fitting procedure and the model would not fit the data), the Gompertz growth model could be used to describe the growth of gulf menhaden larvae from each cruise and transect (Figs. 5-7, Table 2). The growth model for the FL December 1980 larvae approximates an exponential form because of the exceptionally low value for α. This may be due to the preponderance of small, young larvae.

GROWTH COMPARISONS

Louisiana - Seasons and Years

There were statistically significant differences (MANOVA, $P < 0.001$) in the growth curves for larvae caught off Louisiana for two seasons (December, February) and three years (1979-80, 1980-81, 1981-82). To determine if differences existed between seasons in each year and among any two years within each season, I selected 9 of the possible 15 pairwise comparisons for testing. The Bonferroni critical value in these tests was 0.0033 (0.05/15). The inability to fit a Gompertz growth model to the TX December 1981 data precluded a comparison with the larvae collected off Texas in February 1982.

Pairwise comparisons for within years data for Louisiana larvae showed significant differences ($P < 0.003$) in growth curves between early season (December) and late season (February) for each year. Faster growth of early season larvae is evident if the respective curves (Figs. 5; 6a, c; 7a, c) are compared. For any age, the predicted size is greater for early season than for late season larvae. Only for the third year did the length at age 40+ days of February-caught larvae exceed that for December-caught larvae.

In similar comparisons for larvae caught off Louisiana in December of all three years, there were significant differences ($P < 0.003$) in the growth curves (Figs. 5a, 6a, 7a) for any two years. As judged by the predicted size at any age, larvae appeared to grow faster in 1979 than in either 1980 or 1981. While the curves for the 1980 and 1981 larvae overlapped, larvae from 1980 were larger at 30+ days than were the 1981 larvae. Significant differences were also found among the curves (Figs. 5b, 6c, 7c) for larvae caught in

TABLE 2.—Estimates of Gompertz growth model parameters and mean age (days) and mean SL (mm) for larval gulf menhaden collected in the northern Gulf of Mexico during the winters 1979-80, 1980-81, and 1981-82. R^2 is the coefficient of determination for the respective models.

Date	Transect[1]	Number fish aged	R^2	Growth model parameters[2] $L_{(0)}$	$A_{(0)}$	α	Mean estimated age (d)	Mean SL (mm)
Winter 1979-80								
Dec. 1979	LA	42	0.863	2.768 (1.270)	0.1701 (0.0711)	0.0809 (0.0190)	28.1	17.4
Feb. 1980	LA	324	0.954	2.131 (0.138)	0.1592 (0.0105)	0.0710 (0.0031)	30.2	12.7
Winter 1980-81								
Dec. 1980	LA	191	0.931	2.888 (0.188)	0.1125 (0.0097)	0.0496 (0.0044)	22.0	11.8
Dec. 1980	FL	80	0.701	3.418 (0.994)	0.0561 (0.0370)	0.0001 (0.0407)	14.9	7.9
Feb. 1981	LA	338	0.849	2.702 (0.231)	0.1159 (0.0120)	0.0577 (0.0049)	24.6	11.7
Feb. 1981	TX	223	0.526	5.839 (0.579)	0.0305 (0.0088)	0.0125 (0.0110)	21.5	10.3
Winter 1981-82								
Dec. 1981	LA	370	0.921	0.384 (0.076)	0.4780 (0.0433)	0.1240 (0.0054)	21.7	13.3
Dec. 1981	TX	114	—	—[3]	—[3]	—[3]	25.4	11.9
Feb. 1982	LA	191	0.736	0.807 (0.337)	0.2729 (0.6093)	0.0851 (0.0090)	31.2	15.5
Feb. 1982	FL	88	0.624	2.278 (0.824)	0.1067 (0.0454)	0.0394 (0.0205)	17.6	8.9
Feb. 1982	TX	42	0.946	1.798 (0.392)	0.1276 (0.0340)	0.0500 (0.0142)	22.5	10.0
All years								
All data pooled		2,003	0.822	2.355 (0.098)	0.1345 (0.0059)	0.0608 (0.0020)	24.4	12.6

[1]LA=Mississippi River Delta (Southwest Pass Louisiana); FL=Cape San Blas, FL; TX=Galveston, TX.
[2]$L_{(0)}$=length at hatching, $A_{(0)}$=specific growth rate at hatching, α=exponential decline in $A_{(0)}$. Values in parentheses are estimated standard errors from the nonlinear regressions.
[3]Gompertz growth model did not fit the data.

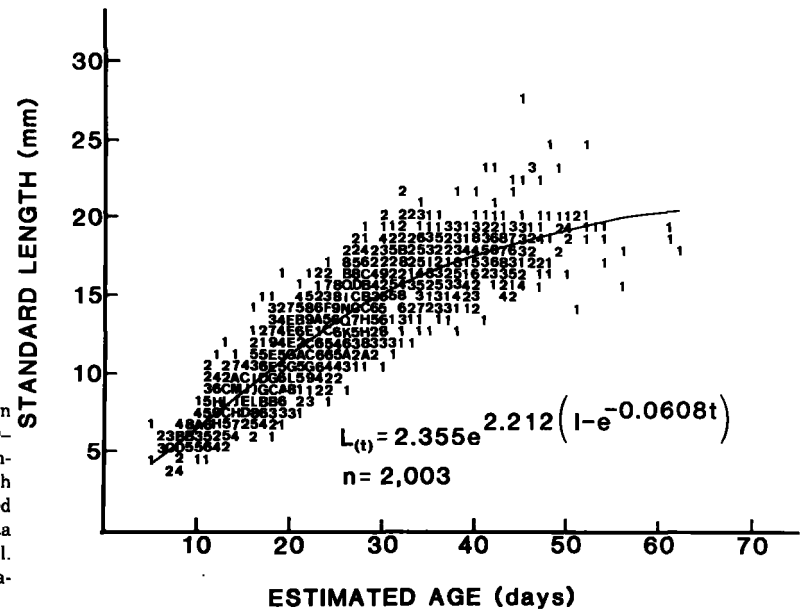

FIGURE 4.—Growth of gulf menhaden larvae collected in the winters of 1979–80, 1980–81, and 1981–82 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the pooled data. Two through nine coincident data points are labelled with their numeral. Coincident points of 10 and above are labelled A, B, etc.

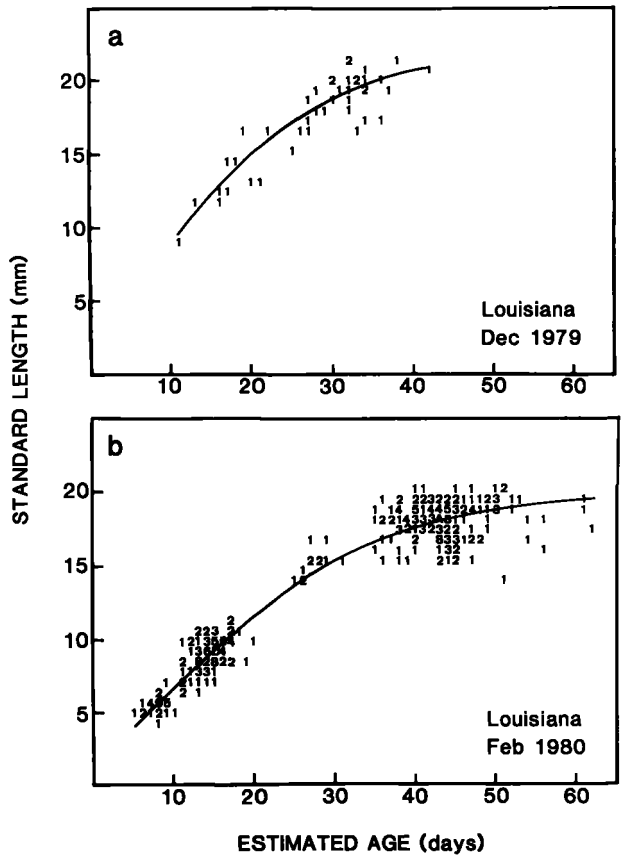

FIGURE 5.—Growth of larval gulf menhaden collected in the winter 1979–80 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

February in three years. Larvae caught in 1980 grew faster than larvae caught in 1981 and larvae caught in 1982 up to 25 days, thereafter 1980 and 1982 had very similar size at age estimates.

Louisiana vs. Florida vs. Texas - February 1982

There were no significant differences (MANOVA, $P = 0.212$) among the growth curves for larvae caught in February 1982 off Louisiana, Texas, and Florida (Figs. 7c, d, e), and hence no pairwise comparisons were necessary.

Louisiana vs. Texas - February 1981–82

Statistically significant differences (MANOVA, $P < 0.002$) in larval growth were observed in the LA and TX transects from February 1981–82. Pairwise comparisons indicated significant differences ($P < 0.008$) in the growth of larvae collected off Texas in 1981 (Fig. 6d) and 1982 (Fig. 7e) and in growth between LA 1981 (Fig. 6c) and TX 1981 collections. The earlier pairwise comparisons had already shown a significant difference in growth of larvae from LA February 1981 and February 1982 collections (Fig. 7c), but none for growth of larvae caught in the LA February 1982 and TX February 1982 collections. Two other potential tests, between transects of different areas and different years, were not considered to be meaningful.

Larvae caught off Louisiana in February 1981 were larger at age 18+ days than were larvae caught off Texas in February 1981, and might be considered to be faster growing fish. There was a

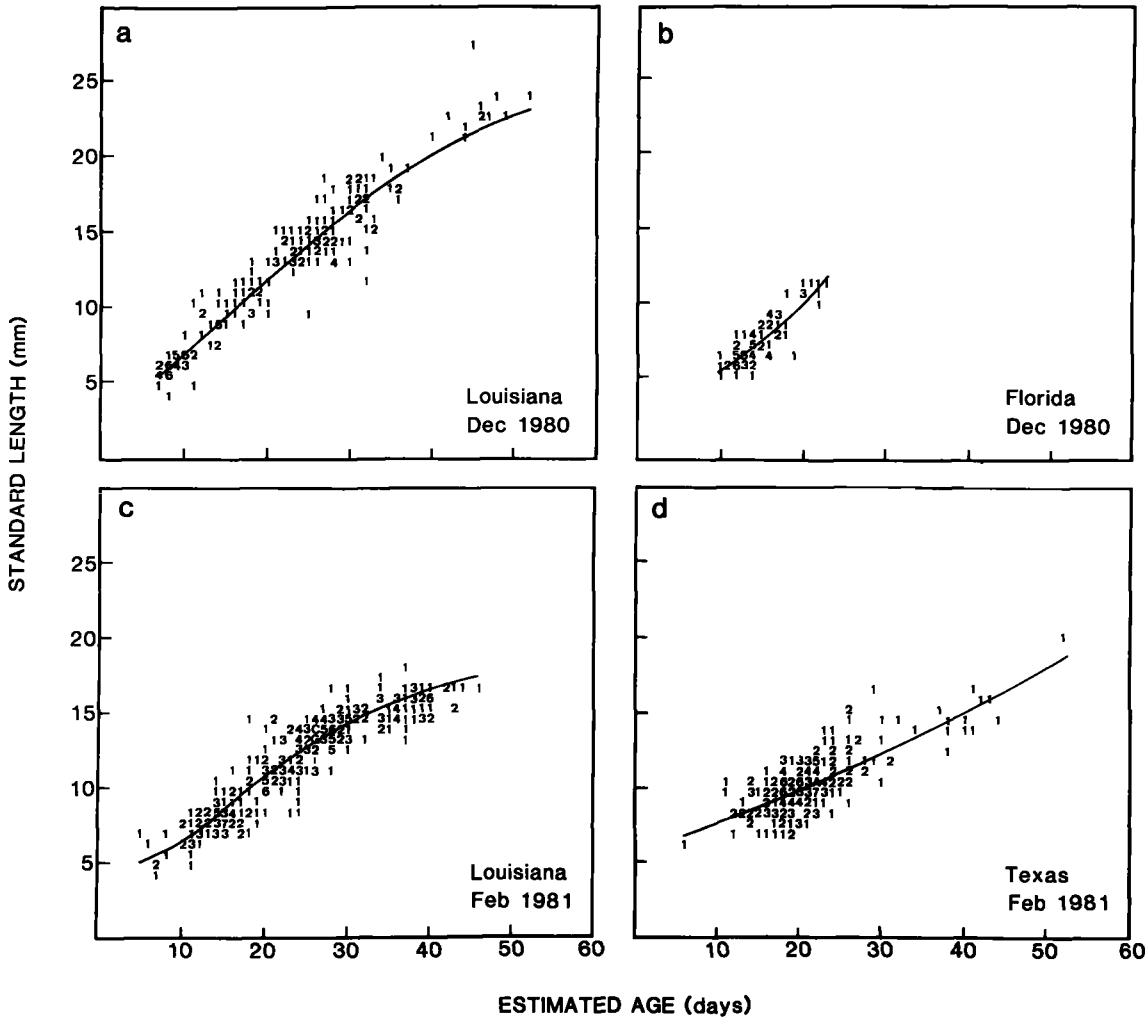

FIGURE 6.—Growth of larval gulf menhaden collected in the winter 1980–81 in the northern Gulf of Mexico. The Gompertz growth model was used to describe the data. Coincident data points are labelled as in Figure 4.

statistical difference in growth of larvae caught off Texas in February 1981 and 1982, and it appears that the 1982 larvae grew at a faster rate. Conclusions from these statistical differences involving TX February 1981 larvae collections should be viewed with caution because of the relatively poor fit ($r^2 = 0.526$) of the model. Inadequacies, such as the lack of larvae <13 or >31 days old, in that data set probably resulted in the relatively poor parameter estimates (Table 2). Additional sampling would be necessary to further test the hypotheses of differences in growth between geographic areas in the northern Gulf of Mexico and between years for Texas larvae.

Estimated Spawning Times

Gulf menhaden larvae observed in this study were estimated to have been spawned from mid-October to mid-February (Fig. 8). The limited extent of seasonal sampling precluded estimation of the probable total range of the spawning season. Most larvae captured in December and February had been spawned in November and January respectively (Fig. 8). The considerable overlap in spawning times of larvae caught the same month in different years is a reflection of the similarity of sampling dates. The relatively narrow distribution of spawning dates for larvae caught off Flor-

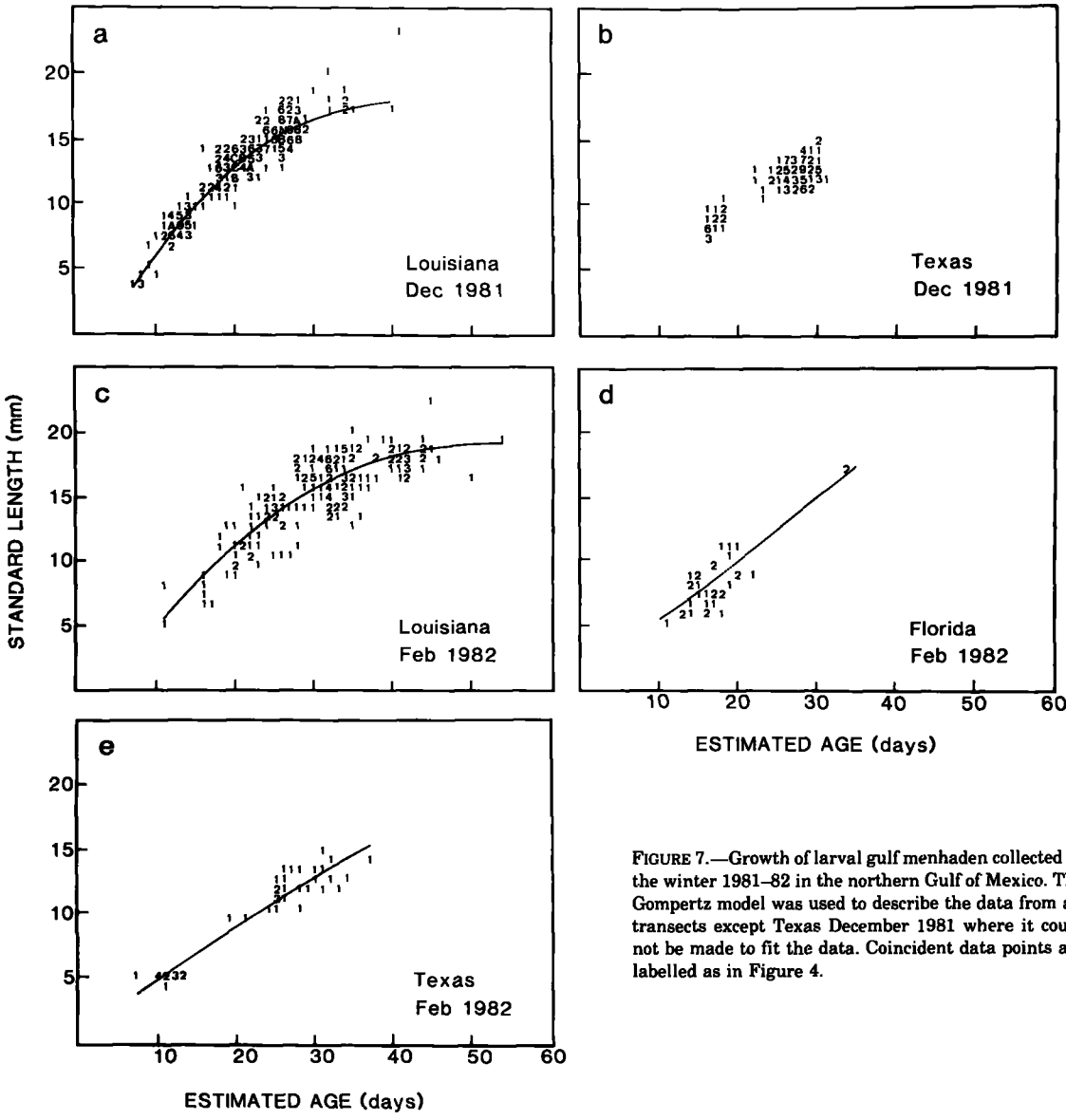

FIGURE 7.—Growth of larval gulf menhaden collected in the winter 1981–82 in the northern Gulf of Mexico. The Gompertz model was used to describe the data from all transects except Texas December 1981 where it could not be made to fit the data. Coincident data points are labelled as in Figure 4.

ida in both December 1980 (Fig. 6b) and in February 1982 (Fig. 7d), off Louisiana in February 1982 (Fig. 7c), and off Texas in February 1981 (Fig. 6d) represent larvae from fewer cohorts.

DISCUSSION

Laboratory observations indicate that larval gulf menhaden on the average form one growth increment per day on their otoliths and that counts of these increments can be used to estimate age. Otoliths of larval gulf menhaden are thin and round, and the increments are generally easily counted and consequently are ideally suited for ageing. The most closely spaced increments, those occurring near the focus, were at least 1.5 μm wide and were above the 0.2 μm resolution of the light microscope (Campana and Neilson 1985). First increment formation occurs about 5 days after spawning and probably coincides with first exogenous feeding. This is supported by Hettler (1984) who found that gulf menhaden eggs hatched at about day 1.7 at 19°-20°C. Four days after hatching larvae had functional

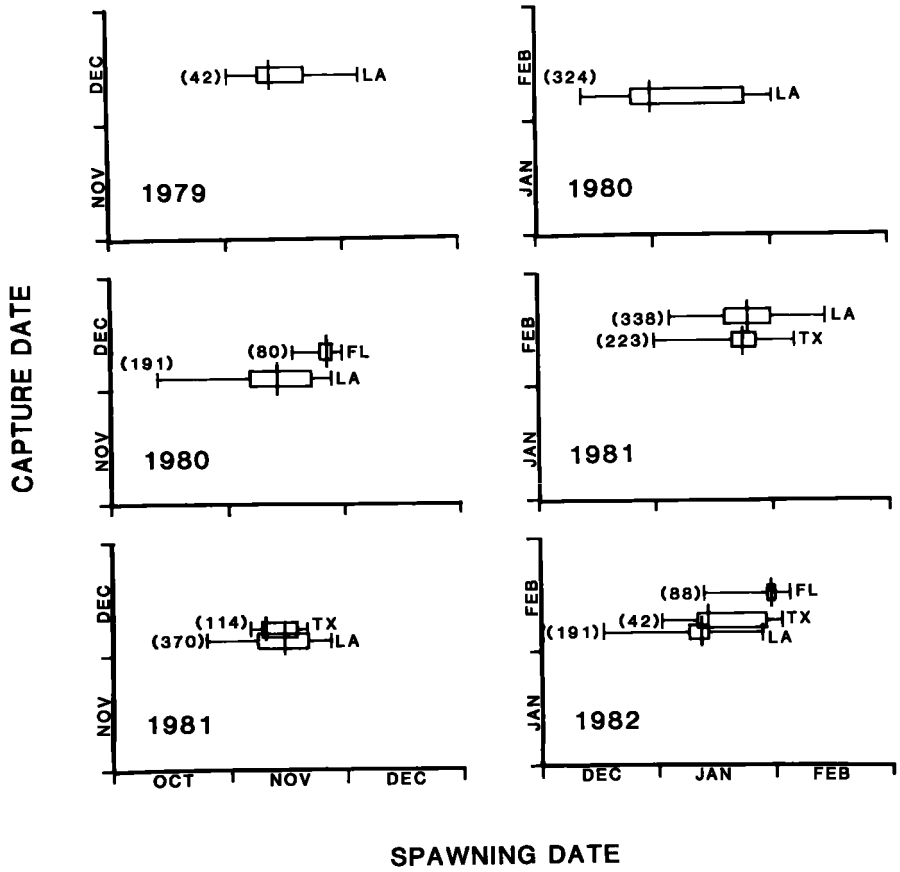

FIGURE 8.—Schematic plots of the spawning times of larval gulf menhaden collected in the northern Gulf of Mexico during 6 cruises of the RV *Oregon II* from December 1979 to February 1982. In each distribution the vertical line is the median value and 50% of the data points fall within the block. Lines beyond the boxes represent the range of data points. The value in parentheses to the left of each distribution is the number of fish.

mouths and were 4.5 mm SL. However, developmental rates are probably temperature dependent (Powell and Phonlor 1986), and hence larvae at lower temperatures would be older at first feeding.

The Gompertz growth model appears to adequately describe the growth of larval gulf menhaden in most cases. Except where data are somewhat limited (Figs. 6b, d; 7b, d) the fit of the model is relatively good and the r^2 is >0.73 for each transect (Table 2). Gompertz growth models have been used (Zweifel and Lasker 1976; Methot and Kramer 1979; Laroche et al. 1982; Warlen and Chester 1985) to describe growth of larval fishes where the length-age plots are nonlinear and upper asymptotes were apparent.

Average growth rate of larval gulf menhaden to day 60 was 0.30 mm/day throughout its oceanic existence. This rate was very similar to that, 0.28 mm/day (estimated from figure 2 of Hettler 1984), for larvae reared in the laboratory at 20° ± 2°C for 60 days. However, wild-caught larvae were from wider extremes in water temperature, with mean early season (December) temperatures from 17.4° to 21.2°C and late season (February) 12.9° to 16.4°C. The growth rate of larval Atlantic herring, *Clupea harengus*, up to 50 days old was similar and varied between 0.23 and 0.30 mm/day (Lough et al. 1982). However, gulf menhaden larvae grew slower than the fast growing but relatively short-lived engraulids—bay anchovy, *Anchoa mitchilli* (Fives et al. 1986) and northern anchovy, *Engraulis mordax* (Methot and Kramer 1979).

Only a small number of larvae from all the collections were ≥50 days old. Larvae of this age

were either not in the sampling area or were inaccessible to the fishing gear used. Although the latter cannot be fully discounted, the former possibility is most likely, since larvae as they grow are known to be transported (Shaw et al. 1985b) toward estuaries. Larvae are about 15–25 mm SL (estimated from Suttkus 1956) when they enter estuaries in Louisiana, and the smallest immigrating larvae are estimated from the growth model (Fig. 4) to have been at least 30 days old. Larvae then are probably 30–70 days old when they enter Gulf of Mexico estuaries. This range is very similar to that for Atlantic menhaden, *B. tyrannus*, entering North Carolina estuaries (S. M. Warlen, unpubl. data). The so-called "larval drift" period for gulf menhaden is probably closer to 4–10 weeks than the 3–5 weeks surmised by Reintjes (1970).

Growth of larval gulf menhaden in the northern Gulf of Mexico varied both spatially and temporally. For three consecutive years there were significant differences in growth for early season (December) and late season (February) larvae caught off the Mississippi River Delta. The increase in length for early season larvae was greater than for larvae hatched in late season. Environmental conditions in this area differed between early season and late season. Mean water temperature measured during the December 1979, 1980, and 1981 cruises were 17.4°, 19.4°, and 21.2°C, respectively, while in February 1980, 1981, and 1982 the temperatures were 13.8°, 15.7°, and 14.7°C, respectively. Although not shown experimentally for gulf menhaden larvae, there is evidence that larvae of some marine fishes grow faster at higher temperatures (Laurence 1978; Laurence et al. 1981). Jones (1985) also associated higher water temperatures with higher growth of larvae and found that increase in length of Atlantic herring larvae hatched early in the season was greater than for larvae hatched late in the season.

Growth rate of larvae caught in the same season but in different years was inversely related to mean water temperature. Larvae caught in December off Louisiana showed a trend of higher growth (1981 < 1980 < 1979) at lower respective mean water temperatures (21.2°, 19.4°, 17.4°C); similarly, the growth rates for larvae caught in February (1981 < 1982 < 1980) was higher at lower respective mean water temperatures (15.7°, 14.7°, 13.8°C). Other environmental factors in addition to temperature may also affect the growth rate of larval menhaden. Food availability that can be an important growth-limiting factor for larval fishes, may be determining the relative growth rates at the lower temperatures in February. On the basis of limited data on the zooplankton (pelecypod larvae, copepod nauplii, copepodites, and adult copepods) that could serve as food for gulf menhaden larvae (Govoni et al. 1983), food availability (number/100 m^3) is highest in February 1980, lower in 1982, and lowest in 1981. Analogous food abundance data is not available for the December cruises, but levels would probably need to be higher on a per fish basis to support the higher metabolism concomitant with the higher December mean water temperatures (17.4°–21.2°C). The main and interaction effects of growth-limiting (food abundance) and growth-regulating (temperature) factors on larval gulf menhaden growth still must be determined experimentally, preferably using laboratory-spawned and -reared larvae.

The apparent growth advantage enjoyed by menhaden larvae spawned early in the season (November) is only typical for a small part of the population. The largest segment of the population, those spawned in the peak months of January and February (Christmas and Waller 1975) and that immigrated to estuaries in February–April, typically had slower growth. Although slower growing, larvae spawned later in the season may be more successful in reaching estuaries. Guillory et al. (1983) found a negative relationship between temperature and gulf menhaden recruitment into Louisiana estuaries. The larger estuarine recruitment later in the season may be related to winter-early spring (January-April) predominant west-northwest longshore flow of coastal water within and just outside the coastal boundary front producing longshore advective transport and of lesser importance by episodic, short-term cross-shelf advection associated with cold fronts (Shaw et al. 1985b). They hypothesized that longshore currents facilitated the movement of larvae toward shore. Only for December did they note a reverse flow (eastward) that would not allow larvae to be transported toward estuaries west of the Mississippi delta.

The between transect comparisons of growth rate of larvae caught off Texas and Louisiana in February showed a difference in 1981 but not in 1982. Again higher growth rates were associated with higher mean water temperatures. Larvae from the LA February 1981 sample ($\bar{x}$ water temperature = 15.7°C) grew faster than larvae from the TX February 1981 sample ($\bar{x}$ water tempera-

ture = 12.0°C). Where no significant differences in growth were found, i.e., between LA and TX February 1982 samples, the respective mean water temperatures were 14.7° and 14.4°C. Neither of those growth curves were significantly different from the curve for larvae from the FL February 1982 sample where the mean water temperature was 16.4°C. However, the paucity of larvae >23 days old caught off Florida in February 1982 (Fig. 7d) suggests that comparisons of that data set with the data sets for larvae caught off Louisiana and Texas in February 1982 would be of little value.

The estimated spawning period for gulf menhaden extended from mid-October to mid-February (Fig. 8). These results agree with Fore (1970) and Christmas and Waller (1975) who, using the occurrence of eggs and larvae, estimated that gulf menhaden spawned from mid-October through March. Gonad weight-body weight ratios of adults (Lewis and Roithmayr 1981) and morphological and physiological features of ovarian tissue (Combs 1969) also indicate that spawning extends from October to early March. Based on the movement of late larvae into Lake Pontchartrain, Suttkus (1956) presumed that gulf menhaden spawning began in October and ceased in February. He suggested that the beginning and end of the spawning period fluctuates from year to year, and that there is no spawning activity during the spring and summer months as Higham and Nicholson (1964) have reported for the closely related Atlantic menhaden.

Most larvae caught in December were spawned in November (Fig. 8) regardless of the year. Larvae caught in February were spawned mostly in January but estimated spawning dates extended from mid-December to mid-February. For any given cruise, larvae from off Texas and Louisiana were spawned at about the same time. There was also considerable overlap in the spawning dates in any cruise off Florida and the other areas. The distribution of the central 50% of spawning dates from the Louisiana sample in February 1980 extended over a 29-d period and was wider than for any other data set. This unusually wide distribution may have been due to the presence of two distinct cohorts, one spawned in late December and one in late January, collected on the February 1980 cruise. Combs (1969) found that this species had intermittent total spawning. Lewis and Roithmayr (1981) inferred that gulf menhaden were intermittent, or fractional spawners. Christmas and Waller (1975) noted a modal temporal distribution of eggs in the region from the Mississippi delta to east of Cape San Blas. Baldauf[4] sampled young menhaden in the lower Neches River, TX, from November through April and found two incoming populations from which he suggested that there may have been two spawning peaks. Only in the larval collections of December 1981 did spawning date distribution appear to be bimodal; 7 and 20 November for Louisiana and 8 and 19 November for Texas. Future sampling throughout the spawning season will be necessary to determine the seasonal periodicity and peaks of gulf menhaden spawning. Relative numbers of larvae in cohorts within the spawning season could then be compared with measurements of environmental conditions as a test of the match-mismatch hypothesis (Cushing 1975) and to further test, as Methot (1983) has done, whether larvae spawned during favorable environmental periods constitute the greatest percentage of the year class.

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SOURCES OF VARIATION IN CATCH PER UNIT EFFORT OF YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA* (STORER), HARVESTED OFF THE COAST OF NEW ENGLAND

LORETTA O'BRIEN AND RALPH K. MAYO[1]

ABSTRACT

Factors affecting variability in commercial catch per unit effort (CPUE) of yellowtail flounder were examined in order to establish a basis for standardizing fishing effort. Analysis of variance (ANOVA) procedures were employed to test for differences in CPUE among vessel tonnage class, fishing area, and depth zone and the interactions between tonnage class and area, and tonnage class and depth. Vessel tonnage class and fishing area accounted for highly significant ($P < 0.01$) sources of variation in CPUE whereas depth was not significant ($P > 0.05$) in most cases. Interactions between tonnage class and stock area were also highly significant in all cases. A series of annual fishing power coefficients was computed for each tonnage class relative to a standard for each stock based on parameter estimates obtained by fitting the CPUE observations to a linear model with tonnage class as the independent variable. Deviations of annual fishing power coefficients from the 20-year mean were found to exhibit significant first order autocorrelations. Consequently, annual coefficients were computed over the entire 1964–83 period by incorporating tonnage class, annual and seasonal effects as independent variables in a three-way linear model. Although the standardized CPUE estimates obtained from this procedure are similar to those obtained by previous methods, the revised procedures described in this paper insure adequate representation of all vessel classes engaged in the yellowtail fishery in the CPUE calculations.

Fishing effort and resulting catch per unit effort (CPUE) indices are routinely used in assessing the impact of commercial fishing operations on stock abundance. The traditional concept that aggregate CPUE indices may be used to measure annual changes in relative stock abundance is based on the principal assumption that the catchability coefficient (q) either remains constant over all fleet components, or that nominal effort is adjusted to account for differences in relative efficiencies (Pope and Parrish 1964; Kimura 1981). Variation in q may be due to persistent differences in fishing power of various types of gear or to technological innovations which may be gradually introduced over time (Gulland 1964; Sissenwine 1978). Biological interactions such as changes in availability of a species due to seasonal distribution patterns or to annual changes in abundance may also affect the overall catchability of demersal species (Garrod 1964; Pope and Garrod 1975). Variability in catchability coefficients may be taken into account by relating nominal fishing effort of each fleet component to some chosen standard category.

Numerous authors have described the basic procedures for calculating relative fishing power of various fleet components. Beverton and Holt (1957) provided evidence to suggest that the distribution of logarithms of fishing power factor/vessel tonnage ratios could be described by a normal curve while Gulland (1956) employed an analysis of variance (ANOVA) model of log CPUE. The properties of the ANOVA model were further examined by Robson (1966) who extended the techniques developed by Gulland (1956) and formally specified the analysis of Beverton and Holt (1957) as a two-way multiplicative ANOVA model. Stern and Hennemuth (1975) employed the method of Robson (1966) in their analysis of fishing effort in the U.S. Georges Bank haddock fishery using depth fished and vessel tonnage as classification variables. In a previous study, Rounsefell (1957) computed standardized log CPUE indices to determine relative abundance of several co-occurring species on Georges Bank according to depth. More recently, Gavaris (1980) and Kimura (1981) have developed modifications of the ANOVA model to estimate annual standardized CPUE indices from time series of catch and effort data by incorporating a year effect in the model.

Standardized annual CPUE indices based on

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criteria established by Lux (1964) have been routinely used to monitor relative abundance of three stocks of yellowtail flounder, *Limanda ferruginea* (Storer), in the commercial fishery off the New England coast (Fig. 1). Lux calculated CPUE indices for otter trawlers ranging from <26 gross registered tons (GRT) to 100 GRT based on trips in which yellowtail flounder accounted for 50% or more of the total landed weight between 1942 and 1961. A fishing power coefficient was then computed for each of several GRT categories as the ratio of CPUE to a standard GRT category CPUE for the entire timespan. A separate set of fishing power coefficients was computed for each of the three stocks. Lux's (1964) work improved upon an earlier analysis of yellowtail flounder CPUE by Royce et al. (1959) which was based only on relatively small vessels ranging in size from 5 to 50 GRT that dominated the fishery during the 1940's.

Since 1964, numerous technological innovations have drastically changed the character of the New England fishing fleet as traditional side trawlers have gradually given way to larger, more efficient stern trawlers equipped with sophisticated electronic navigation and hydroacoustic devices. This gradual alteration in the fleet characteristics over time suggests that previously documented relationships among vessel categories may no longer be applicable to the current fishery, and that use of nominal effort in CPUE calculations will tend to overestimate relative abundance in the more recent years (Westrheim and Foucher 1985). Long-term declines in yellowtail flounder abundance on each of the principal fishing grounds (Clark et al. 1984) also indicate that current catchability coefficients may differ from previous values. Accordingly, updated fishing power coefficients are required to adequately assess changes in effective fishing effort and CPUE which have occurred during the past two decades. Further, to obtain annual effort and CPUE estimates over such a broad period of years, techniques for computing relative fishing power should incorporate a time element in the analysis.

In this paper we examine variation in CPUE with respect to fishing area, depth, vessel tonnage class, season, and year for three stocks of yellowtail flounder on Georges Bank, Southern New England, and Cape Cod grounds between 1964 and 1983. Before evaluating differences in relative fishing power among vessel classes, we investigate potential interactions between tonnage class and area and tonnage class and depth within each year, and partition the data to minimize tonnage class-area interactions. For each stock, fishing power coefficients are examined for

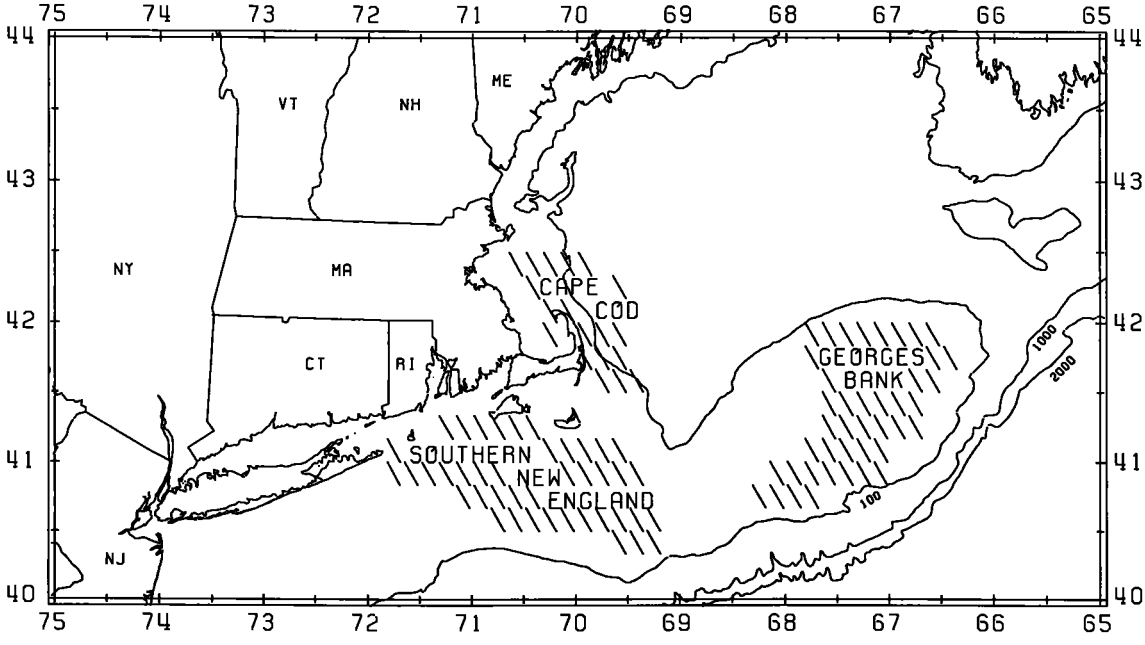

FIGURE 1.—Yellowtail flounder stocks off the coast of New England (After Lux 1963).

annual and seasonal interactions. A three-way linear model, incorporating annual and seasonal components, is employed to compute relative fishing power coefficients over the entire 20-yr period and estimate annual standardized CPUE indices.

DISTRIBUTION OF CATCH AND EFFORT

Commercial exploitation of yellowtail flounder began in the late 1930's following the decline of the winter flounder fishery (Royce et al. 1959). Nominal catches[2] for the three grounds combined rapidly increased to 31,500 metric tons (t) in 1942 but subsequently declined to 5,500 t in 1954. Landings by U.S. vessels gradually increased to a record high of 36,900 t in 1963, but declined again to 10,500 t in 1978 (Fig. 2). Distant water fleet (DWF) catches were also substantial during this period, peaking at 20,700 t in 1969. Overall catches from the three fishing grounds have recently increased to 30,800 t in 1983, although 1984 landings declined to 15,500 t (Clark et al. 1984). The decline in catch during the 1940's was not due to overfishing (Royce et al. 1959) but may have been related to a warming trend in the region which affected recruitment (Sissenwine 1974). The more recent decline between 1969 and 1978, however, has been attributed to increased fishing effort by both domestic and distant water fleets (Brown et al. 1980).

In the early 1940's the size of vessels fishing for yellowtail flounder varied from 5 to 75 GRT. The predominant vessels on Southern New England and Cape Cod grounds ranged from 26 to 50 GRT; on Georges Bank, the dominant vessels were in the 51–75 GRT range. By the mid-1960's larger vessels had begun to enter the fishery, increasing the maximum size to 215 GRT. During this period the size range of the dominant vessels on Southern New England grounds and on Georges Bank had increased to 51–72 and 73–104 GRT, respec-

[2]Nominal catch defined as live weight equivalent of landings, excluding discards.

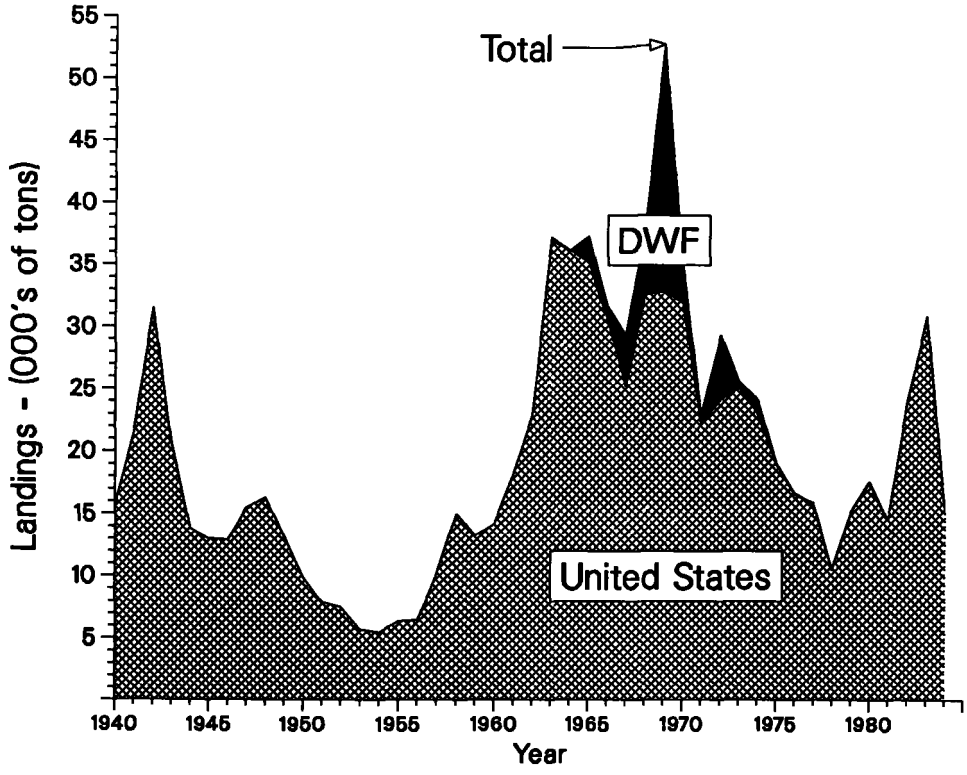

FIGURE 2.—Yellowtail flounder landings (metric tons) by United States and distant water fleet (DWF) vessels from the combined Georges Bank, Southern New England, and Cape Cod grounds, 1940–84.

tively. Vessels fishing the relatively nearshore Cape Cod grounds remained in the 34–50 GRT range. Larger vessels continued to enter the fishery during the 1970's and, by 1983, several vessels were in the 311–400 GRT range. Since 1964, vessel GRT's have been categorized by tonnage class (TC) as given in Table 1a.

A review of Lux's (1964) data from 1942 to 1961 and the distribution of more recent yellowtail flounder landings from 1964 to 1983 (Figs. 3–5) reveal that vessels of similar size have continually fished the same general areas over the past 40 years. The TC 21–24 vessels fish primarily on Southern New England and Cape Cod grounds (Fig. 3), although TC 24 vessels occasionally enter the southwest part of Georges Bank. The TC 25–33 vessels fish on both Georges Bank and Southern New England grounds (Fig. 4), while TC 41–43 vessels concentrate on Georges Bank (Fig. 5). Although TC 41 vessels operate at times on the eastern part of the Southern New England grounds, the TC 42 and 43 vessels fish exclusively on Georges Bank.

The distribution plots (Figs. 3–5) reveal a gradual phaseout of smaller (TC 21–24) vessels on the inshore Southern New England and Cape Cod grounds and a concurrent increase in the activity of large (TC 41–43) vessels on Georges Bank, Southern New England, and, to a lesser extent, on the Cape Cod grounds. In evaluating trends in CPUE we must ask whether these changes in the yellowtail fishery over the past 20 years (i.e., the shift in the predominant vessel size on two of the three grounds and the addition of larger vessels to the fleet on all three grounds) affect CPUE as calculated by the traditional method (Lux 1964). If the same size range of vessels (5–100 GRT) had fished for yellowtail flounder throughout the years, a shift in the dominant vessel class would not affect CPUE estimates since effort would be standardized against the same class and is, therefore, relative. However, the maximum vessel size has increased and the predominant TC now represents vessels larger than 100 GRT. Since landings and effort data contributed by these larger vessels were not incorporated into previous CPUE calculations, CPUE estimates will not necessarily represent overall fleet performance in recent years. The following procedures, therefore, were developed to calculate new fishing power coefficients that encompass the entire size range of vessels currently in the fishery.

TABLE 1.—Definition of vessel tonnage classes (a) and depth ranges and corresponding zones (b) included in analysis of variance of yellowtail flounder CPUE.

a	Gross registered tonnage (range)	Vessel tonnage class
	5–10	21
	11–15	22
	16–22	23
	23–33	24
	34–50	25
	51–72	31
	73–104	32
	105–150	33
	151–215	41
	216–310	42
	311–400	43
b	Depth range (m)	Depth zone
	1–55	1
	56–110	2
	111–183	3

METHODS OF ANALYSIS

Catch and effort data recorded by trip were obtained from Northeast Fisheries Center (NEFC) detailed commercial landings files. Fishing effort or days fished (df) is defined on a 24-h basis as number of hours of actual fishing time divided by 24. Only trips landing 50% or more of yellowtail flounder were analyzed; trips included within the qualification level generally accounted for 70–90% of the total yellowtail landings over the entire period, except on Cape Cod grounds where qualified trips accounted for 40–60% of the total. Catch per day fished (CPUE) was computed for each trip and transformed to ln CPUE since preliminary analysis indicated a positive correlation of the arithmetic mean CPUE with the variance. Use of the log transformation, however, stabilized the variance and created a lognormal distribution as noted by Gulland (1956) and Steel and Torrie (1980).

Trips landing between 1964 and 1983 are classified in the data base by vessel tonnage class, statistical area, and depth zone fished. Vessels ranging in size from 5 to 310 GRT (Table 1a) and statistical areas corresponding to the three major stocks were selected for analysis as follows: Georges Bank (areas 522–525), Southern New England (area 526 and 537–539), and Cape Cod (areas 514 and 521) (Fig. 6). Because of their sporadic representation, TC 21–23 vessels have been excluded from the Georges Bank analyses and have been combined as one category on the Southern New England grounds. Depth zones 1, 2, and

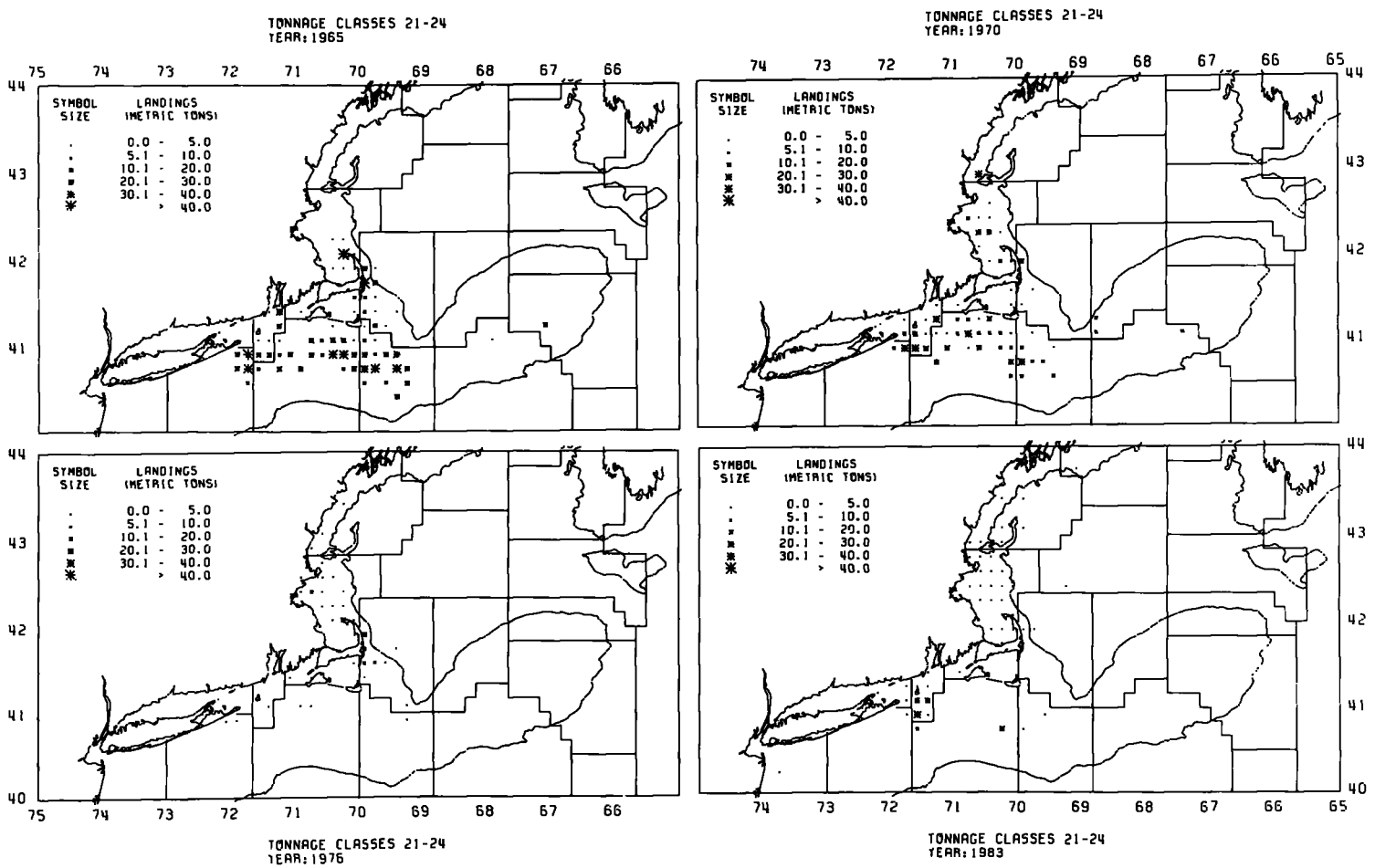

FIGURE 3.—Distribution of yellowtail flounder landings in 1965, 1970, 1976, and 1983 for vessel tonnage classes 21–24.

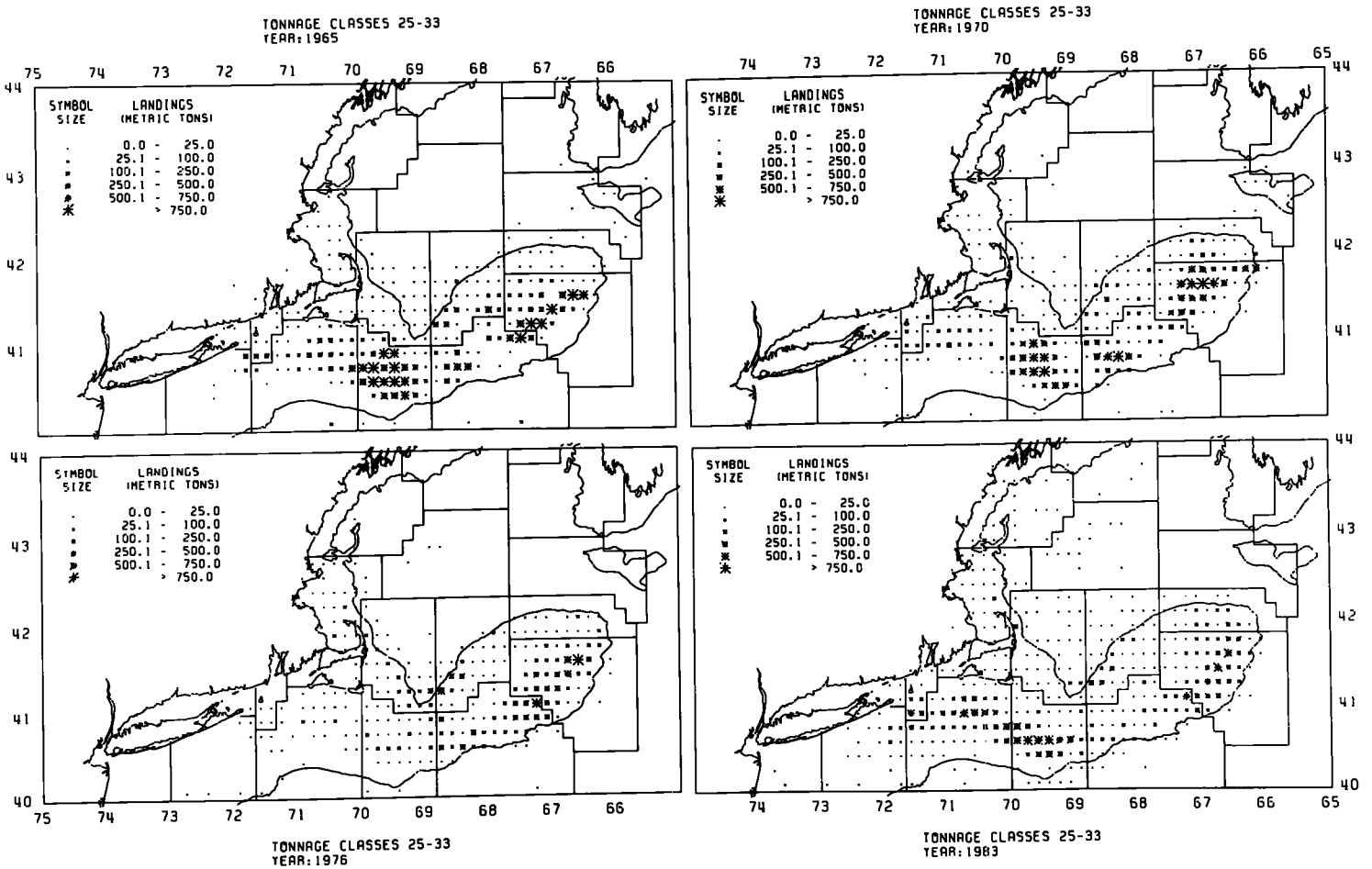

FIGURE 4.—Distribution of yellowtail flounder landings in 1965, 1970, 1976, and 1983 for vessel tonnage classes 25–33.

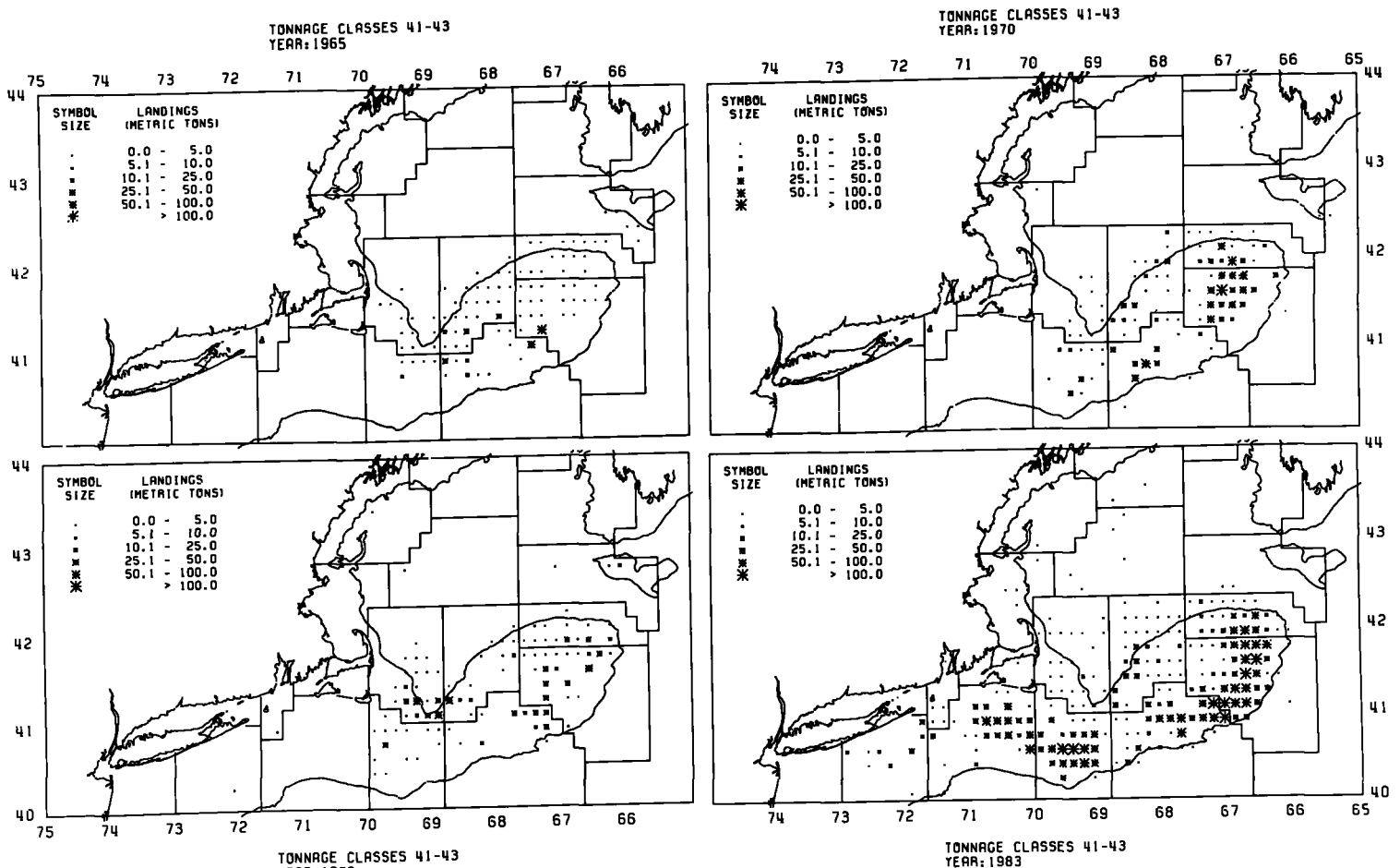

FIGURE 5.—Distribution of yellowtail flounder landings in 1965, 1970, 1976, and 1983 for vessel tonnage classes 41–43.

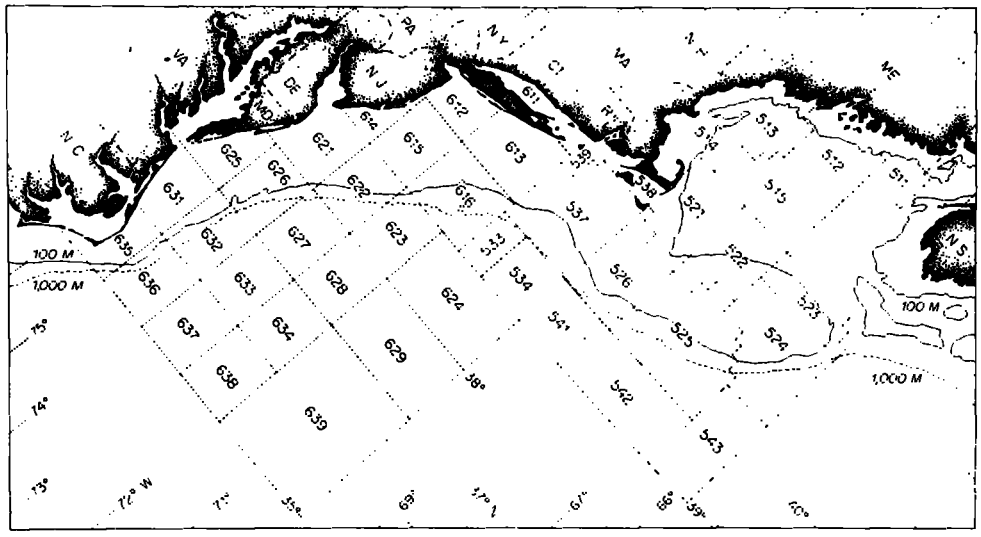

FIGURE 6.—Yellowtail flounder fishing grounds defined by U.S. statistical area are as follows: Southern New England, 526–539; Georges Bank, 522–525; Cape Cod, 514 and 521.

3 (Table 1b) were also selected from six possible zones based on the bathymetric distribution of yellowtail flounder.

Trip data were aggregated at different levels of spatial resolution to examine variability in CPUE over the entire region and within each of the three established stocks. Two-way ANOVAs with interaction were performed on annual data sets using the BMDP statistical software program P4V (Dixon 1981). Given the large number of observations in each analysis, the more rigorous 99% significance level was chosen to test the null hypothesis (no significant differences) since relatively small differences in mean CPUE can produce statistically significant results. The ANOVA was performed initially to test for differences in CPUE among all tonnage classes and statistical areas and to determine the overall extent of tonnage class-area interactions. Secondary analyses were performed to examine the effect of tonnage class-area and tonnage class-depth interactions among and within each of the stocks. All subsequent tests for significance of tonnage class, area, and depth main effects were performed with the interaction effects absorbed in the error sum of squares. Estimates of annual geometric mean CPUE were obtained by combinations of tonnage class, stock area, and depth from the row and column means provided by the P4V software (Tables 2, 3).

A standard vessel class was selected for each of the three stocks for use in calculation of fishing power coefficients based on the prevalence of the vessel class in the fishery and its relative contribution to the landings over the 20 years. The TC 32 category was chosen as the standard for both Georges Bank and Southern New England stocks, and the TC 25 class was chosen as the standard for the Cape Cod stock. Within each stock annual fishing power coefficients were derived for each tonnage class relative to the standard by fitting ln CPUE to a one-way linear model using the GLM procedure of the Statistical Analysis System (SAS Institute 1982) as follows:

$$U = \alpha + \sum_j [\beta_j X_j] + \epsilon.$$

Annual deviations of the coefficients from the 20-yr mean were tested for first order autocorrelation using the Durbin-Watson test statistic (Neter and Wasserman 1974). A time component was subsequently incorporated in the linear model to account for annual trends in the data; seasonal effects were also included by classifying the data according to calendar quarter. The initial year (1964) and the fourth quarter were selected as reference categories. The general model is specified as:

TABLE 2.—Geometric mean CPUE[1] (landings per day fished, metric tons) for Georges Bank, Southern New England, and Cape Cod yellowtail flounder trips by vessel tonnage class, 1964–83.

Year	Vessel tonnage class 21	22	23	24	25	31	32	33	41	42
Georges Bank										
1964	—	—	—	3.65	4.17	4.88	5.04	4.58	4.52	2.14
1965	—	—	—	2.41	3.06	3.62	3.55	3.39	4.97	—
1966	—	—	1.18	1.25	2.27	2.76	2.78	2.76	2.71	—
1967	—	—	—	—	2.20	2.74	2.96	2.78	2.65	—
1968	—	—	—	3.88	2.99	3.47	3.55	3.84	3.53	2.66
1969	—	—	—	3.28	2.82	3.06	3.30	3.02	2.81	3.88
1970	—	—	—	3.74	2.40	2.88	3.08	2.81	2.70	—
1971	—	—	—	1.66	2.07	2.70	2.52	2.24	2.35	—
1972	—	—	—	—	1.96	2.24	2.39	2.29	1.96	—
1973	—	—	—	1.38	2.64	2.61	2.81	3.05	2.76	3.20
1974	—	2.52	—	—	2.79	2.13	2.23	2.19	1.30	3.42
1975	—	—	—	1.93	1.91	1.64	1.93	2.04	1.72	3.19
1976	—	—	—	1.35	1.69	1.77	1.84	2.16	2.06	—
1977	—	—	—	—	1.17	1.66	1.77	2.26	1.81	—
1978	—	—	—	—	1.67	1.50	1.72	2.03	2.82	—
1979	—	2.69	—	1.31	1.80	2.41	2.37	2.82	3.64	—
1980	—	0.30	—	1.09	0.90	2.88	2.62	3.27	3.00	—
1981	—	—	—	1.12	1.24	1.98	2.48	2.61	2.23	—
1982	—	—	1.88	0.48	2.02	1.71	2.10	2.53	3.97	2.07
1983	—	—	—	—	0.79	2.46	1.97	2.21	3.79	—
Southern New England										
1964	2.34	1.94	6.15	4.88	4.66	4.44	5.04	4.59	4.09	—
1965	1.77	1.55	3.87	3.62	3.12	3.56	3.81	4.05	1.50	—
1966	1.21	3.06	3.19	2.93	2.52	2.61	2.56	2.35	3.03	—
1967	1.80	1.14	2.94	3.38	3.23	2.67	2.66	2.31	1.80	—
1968	2.24	4.15	4.69	4.42	4.02	3.41	3.62	3.63	3.53	—
1969	2.65	3.72	5.17	3.81	4.10	3.39	3.43	4.01	2.81	—
1970	7.74	3.28	4.76	3.77	3.96	3.08	3.64	2.87	2.70	—
1971	11.72	1.60	4.06	3.14	3.32	2.85	2.87	3.16	2.35	—
1972	—	1.96	3.19	2.62	3.30	3.01	2.96	3.04	1.96	—
1973	—	1.01	1.05	2.26	2.66	2.29	2.22	2.12	2.76	—
1974	—	1.08	1.62	2.31	2.14	2.07	2.07	2.64	1.30	—
1975	—	0.57	1.57	1.13	1.29	1.33	1.55	1.55	1.72	—
1976	—	0.72	0.90	0.53	0.86	1.13	1.32	1.69	2.06	—
1977	—	0.93	1.73	1.44	1.77	1.61	1.82	1.98	1.81	—
1978	—	—	2.72	1.15	1.58	1.52	2.04	2.26	2.82	—
1979	0.79	1.74	2.28	1.59	2.17	2.32	2.93	2.88	3.64	—
1980	—	1.02	2.46	1.91	2.54	2.68	2.81	3.07	3.00	—
1981	—	1.88	2.50	1.43	2.58	2.76	2.61	3.28	2.23	—
1982	2.49	1.96	2.42	2.29	3.10	3.20	3.72	3.98	3.97	—
1983	8.81	1.74	2.51	3.35	3.43	3.27	3.65	3.57	3.79	—
Cape Cod										
1964	—	1.65	1.38	1.94	2.64	2.85	2.76	—	—	—
1965	—	1.45	1.20	1.59	2.16	3.56	2.12	2.07	—	—
1966	1.13	1.07	1.23	1.48	2.55	3.64	1.76	—	—	—
1967	—	0.78	0.90	1.56	2.46	3.21	1.95	2.62	—	—
1968	—	1.16	0.99	1.89	2.65	4.11	2.42	—	1.13	—
1969	—	1.66	1.33	2.02	2.77	3.64	2.47	—	—	—
1970	—	1.03	1.05	2.34	2.33	3.64	[2]6.96	[2]34.18	2.91	—
1971	—	1.17	1.89	2.43	2.04	2.24	1.90	2.45	3.36	—
1972	1.71	1.63	1.16	2.02	1.85	2.02	1.46	1.79	1.93	—
1973	1.02	1.32	1.06	1.87	1.99	1.90	1.91	1.63	2.84	—
1974	0.83	1.15	0.90	1.59	2.08	1.74	1.82	1.87	1.37	—
1975	0.77	1.13	1.23	1.42	1.92	1.45	1.64	1.09	1.19	—
1976	0.34	1.31	1.38	1.69	1.93	1.42	1.54	1.88	2.15	—
1977	0.28	0.86	1.25	1.50	2.03	1.45	1.42	2.19	2.57	—
1978	—	0.84	1.59	1.90	2.11	1.96	1.53	1.92	5.99	—
1979	0.98	0.91	1.42	1.83	2.10	2.24	1.74	2.23	3.12	—
1980	0.26	0.58	1.30	1.73	2.18	2.24	2.07	2.19	3.34	—
1981	0.70	0.76	1.17	1.69	2.24	2.40	1.22	1.85	2.99	—
1982	0.54	0.71	1.22	1.79	2.02	2.41	1.57	1.94	2.37	—
1983	0.69	1.51	1.23	1.96	1.91	1.29	1.53	1.46	0.83	—

[1]Calculated as $\exp\left[1/n \cdot \Sigma \ln\left(\frac{\text{landings}}{\text{effort}}\right)\right]$

[2]Only one trip by tonnage classes 32 and 33 in 1970 on Cape Cod grounds.

$$U = \alpha + \sum_{ij} [\beta_{ij} X_{ij}] + \epsilon$$

where U = ln CPUE,

α = intercept estimate,

β_{ij} = model parameter estimates in logarithmic units for category j for tonnage class, season, and year,

X_{ij} = dummy variable for tonnage class, season, and year (=1 when category j occurs; = 0 otherwise), and

ϵ = error term.

All tests for significance of main effects were based on the above model without interaction. Separate ANOVAs were also performed to examine first order interactions. Parameter estimates obtained from the model without interaction were retransformed following methods described by Bradu and Mundlak (1970) to derive unbiased fishing power, seasonal, and annual coefficients. Annual coefficients corresponding to the 1965–83 period were multiplied by the reference year CPUE to compute annual standardized CPUE estimates.

RESULTS

Smaller vessels (TC 21–24) generally exhibited the lowest CPUE indices in all three areas, although TC 21–23 vessels were not represented on Georges Bank (Table 2). Catch rates of medium vessels (TC 25; 31–33) were similar to each other, and were generally greater than those for TC 21–24 vessels. Mean CPUE indices for the largest vessels (TC 41 and 42) were more variable, but generally were equal to or greater than those

TABLE 3.—Geometric mean CPUE[1] (landings per day fished, metric tons) for Georges Bank, Southern New England, and Cape Cod yellowtail flounder trips by depth zone, 1964–83.

	Georges Bank				Southern New England				Cape Cod			
	Depth zone				Depth zone				Depth zone			
Year	1	2	3	Combined	1	2	3	Combined	1	2	3	Combined
1964	3.92	4.91	2.74	4.80	5.05	4.96	4.71	5.03	2.13	2.36	—	2.25
1965	3.76	3.48	—	3.55	3.61	3.88	2.28	3.66	1.61	1.80	2.36	1.71
1966	3.02	2.62	1.29	2.71	2.71	2.66	0.71	2.71	1.99	2.13	1.70	2.07
1967	3.19	2.69	2.81	2.79	2.97	2.77	1.14	2.91	1.52	2.16	—	1.80
1968	3.38	3.51	—	3.49	3.70	3.97	3.24	3.76	2.15	2.31	—	2.24
1969	3.36	3.11	—	3.16	3.62	3.93	1.58	3.66	2.16	2.66	—	2.27
1970	2.81	2.99	1.00	2.93	3.44	3.68	1.62	3.49	1.10	2.24	[2]34.18	1.40
1971	2.20	2.30	2.75	2.28	3.26	2.96	—	3.14	1.03	1.94	—	1.46
1972	2.28	2.37	1.34	2.35	3.28	3.25	2.74	3.27	1.56	1.88	—	1.82
1973	2.30	3.06	2.85	2.91	2.41	2.55	4.40	2.47	1.75	1.83	2.27	1.81
1974	2.10	2.32	2.90	2.30	2.31	2.02	—	2.19	1.86	1.78	—	1.82
1975	1.85	1.99	1.29	1.98	1.59	1.63	—	1.60	1.53	1.38	1.32	1.46
1976	1.75	2.06	—	2.03	1.34	1.56	—	1.43	1.54	1.88	2.93	1.70
1977	1.92	2.15	1.67	2.14	1.92	1.97	—	1.94	1.70	1.89	1.27	1.77
1978	1.78	2.09	1.98	2.07	2.45	2.17	—	2.32	1.90	1.71	3.49	1.86
1979	2.47	2.79	2.04	2.74	2.88	2.39	—	2.76	2.03	2.03	2.47	2.03
1980	2.58	3.50	1.53	3.37	2.71	3.51	1.13	3.04	2.06	2.31	2.38	2.16
1981	2.26	2.88	1.54	2.76	2.46	2.78	—	2.58	1.74	1.96	5.67	1.79
1982	2.34	2.66	2.53	2.62	3.20	3.54	4.53	3.31	1.81	1.44	0.91	1.67
1983	1.98	2.28	3.04	2.26	3.08	3.13	5.91	3.10	1.70	1.41	—	1.62

[1]Calculated as $\exp\left[1/n \cdot \Sigma \ln\left(\frac{\text{landings}}{\text{effort}}\right)\right]$.

[2]Only one trip in depth zone 3 in 1970 on Cape Cod grounds.

corresponding to medium and small vessels, particularly in the later years (Table 2). The initial ANOVAs performed over all statistical areas revealed highly significant ($P < 0.01$) differences in CPUE for tonnage class and area main effects in each of the 20 years (Table 4). The interaction of tonnage class and area was also highly significant in all years, suggesting that relative fishing power of the individual vessel classes varies according to area. ANOVA results for the comparison of CPUE among stocks were highly significant for area main effects in 19 out of 20 years, and the tonnage class-stock area interaction term was highly significant in all years (Table 4). Grouping the data according to stock tended to reduce the amount of significant tonnage class-area interaction within each stock, although differences among tonnage classes remained highly significant.

On Georges Bank the differences in CPUE were highly significant for statistical area and tonnage class main effects in 80 and 100% of the years, respectively, while the tonnage class-area interaction was highly significant in only 40% of the years. Differences due to area on Southern New England grounds were highly significant in all years except 1978, and differences due to tonnage class were highly significant in all years. The interaction term was highly significant in 70% of the years. Differences due to area on the Cape Cod grounds were highly significant in all years except 1975, and differences due to tonnage class were highly significant for all years. The interaction was highly significant in only 35% of the years (Table 4).

Differences in CPUE by depth zone were generally not significant. Depth main effects yielded

TABLE 4.—Frequency with which highly significant ($P < 0.01$) results were obtained from analysis of variance (ANOVA) tests of yellowtail flounder annual CPUE data. (Total number of years tested = 20.) N/A = Not applicable (tests not performed).

	Main effects		
	Area	Tonnage class	Depth
All areas	20/20	20/20	N/A
Among stocks	19/20	N/A	N/A
Within stocks			
Georges Bank	16/20	20/20	10/20
So. New England	19/20	20/20	7/20
Cape Cod	19/20	20/20	3/20

	Interactions	
	Tonnage class × area	Tonnage class × depth
All areas	20/20	N/A
Among stocks	20/20	N/A
Within stocks		
Georges Bank	8/20	4/20
So. New England	14/20	2/20
Cape Cod	7/20	1/20

highly significant differences in only 50, 35, and 15% of the years for Georges Bank, Southern New England, and Cape Cod grounds, respectively (Table 4), while the tonnage class-depth interaction was highly significant in no more than 20% of the years on each of the three grounds.

Interaction between tonnage class and statistical area throughout the region was highly significant in all cases. Further analyses yielded highly significant differences in CPUE among the three stocks and highly significant tonnage class-stock interactions which suggests that relative fishing power among vessel classes is not consistent from stock to stock, implying a need for computing a separate set of fishing power coefficients for each stock. Within each stock, differences in CPUE among statistical areas and tonnage classes were also highly significant in most cases, although the tonnage class-area interaction was not.

Standardized CPUE

Annual fishing power coefficients, obtained by retransforming linear model parameter estimates for each tonnage class, are presented in Table 5 by stock. Cursory examination of the coefficients reveals distinct trends throughout the 20-yr series. On Georges Bank and Southern New England grounds, fishing power coefficients for the smaller vessels (TC 23–25) relative to the standard declined over time, whereas coefficients for the larger vessels increased over time. On Cape Cod grounds the coefficients increased for the smaller vessels (TC 23 and 24) although trends were less pronounced. These trends are illustrated graphically by plotting annual deviations from the 20-yr average in Figures 7–9. A Durbin-Watson test for first order autocorrelation of the annual deviations (Neter and Wasserman 1974) was significant for most tonnage classes within each of the stocks, suggesting the presence of a substantial tonnage class-time interaction.

The three-way linear model, modified to include interaction terms, also revealed highly significant tonnage class-year as well as tonnage class-season and year-season interactions within each of the three stocks (Table 6). When interactions are significant, they can be examined in detail or absorbed in the error term when testing for main effects. Since tonnage class effects have already been examined on an annual basis, the interaction terms were excluded from the three-way model used to obtain parameter estimates for tonnage class, season, and year. The model is specified as follows:

$$U = \alpha + \sum_j [\beta_{1j} X_{1j} + \beta_{2j} X_{2j} + \beta_{3j} X_{3j}] + \epsilon$$

where $\beta_{1j}, \beta_{2j}, \beta_{3j}$ = model parameter estimates in logarithmic units for category j for tonnage class, season, and year,

X_{1j}, X_{2j}, X_{3j} = dummy variables for tonnage class, season, and year (= 1 when category j occurs; = 0 otherwise).

ANOVA results obtained without interaction are presented in Table 6 for each of the three stocks. For Georges Bank and Southern New England stocks, year accounts for the greatest reduction in error sums of squares; on Cape Cod grounds tonnage class accounts for the greatest overall reduction.

Coefficients for tonnage class, year, and season, derived from model parameter estimates for the combined 1964–83 period are presented in Table 7. Tonnage class coefficients for Georges Bank and Southern New England are relatively homogeneous, as compared with those obtained for Cape Cod grounds, owing to the narrower range of vessel tonnage classes which have consistently exploited these fisheries. Seasonal coefficients exhibit the same pattern on Georges Bank and Southern New England with the highest catch rates occurring during the third quarter; on Cape Cod grounds the highest catch rates occur during the second quarter. Trends in annual coefficients are similar on all three grounds. Standardized CPUE indices based on the annual coefficients are illustrated in Figure 10, and traditional indices based on the methods of Lux (1964), as given by Clark et al. (1984), are also presented for comparative purposes.

Although each series indicates similar trends, CPUE indices obtained from the linear model for Georges Bank and Southern New England have remained slightly higher than the traditional indices since the early 1970's. Prior to this, the traditional CPUE indices were greater than the revised indices. On Cape Cod grounds, differences between the two series are considerably greater, particularly in the early years.

TABLE 5.—Annual fishing power coefficients calculated by vessel tonnage Georges Bank, Southern New England,

Year	Vessel tonnage class[1]									
	21	22	23	24	25	31	32	33	41	42
				Georges Bank						
1964				0.73	0.83	0.97		0.91	0.90	0.43
1965				0.68	0.86	1.02		0.95	1.40	—
1966				0.45	0.81	0.99		0.99	0.97	—
1967				—	0.74	0.93		0.94	0.89	—
1968				1.09	0.84	0.98		1.08	0.88	0.75
1969				0.99	0.85	0.93		0.92	0.95	1.17
1970				1.21	0.78	0.94		0.91	0.94	0.92
1971				0.66	0.82	1.07		0.89	1.12	—
1972				—	0.82	0.94		0.96	0.93	—
1973		not		0.49	0.94	0.93	1.00	1.09	1.09	1.14
1974		calculated		—	1.25	0.96		0.98	0.97	1.53
1975				1.00	0.99	0.85		1.06	1.04	1.66
1976				0.73	0.92	0.96		1.17	1.01	—
1977				—	0.66	0.94		1.28	1.67	—
1978				—	0.97	0.87		1.18	1.54	—
1979				0.55	0.76	1.02		1.19	1.35	—
1980				0.42	0.35	1.10		1.25	1.43	—
1981				0.45	0.50	0.80		1.05	1.16	—
1982				0.23	0.96	0.82		1.21	1.41	0.99
1983				—	0.40	1.25		1.12	1.26	—
				Southern New England						
1964	—	[2]0.95	—	0.97	0.92	0.88		0.91	0.81	
1965	—	0.86	—	0.95	0.82	0.93		1.06	0.39	
1966	—	1.12	—	1.14	0.98	1.02		0.92	1.18	
1967	—	0.94	—	1.27	1.22	1.00		0.87	0.68	
1968	—	1.21	—	1.23	1.11	0.94		1.01	0.98	
1969	—	1.32	—	1.11	1.19	0.99		1.17	0.82	
1970	—	1.23	—	1.04	1.09	0.85		0.79	0.74	
1971	—	1.06	—	1.10	1.16	0.99		1.10	0.82	
1972	—	0.99	—	0.88	1.12	1.01		1.03	0.66	
1973	—	0.46	—	1.01	1.20	1.03	1.00	0.95	1.24	

[1]Standard vessel class on Georges Bank and Southern New England rounds = 32. Standard vessel class on Cape Cod grounds = 25.

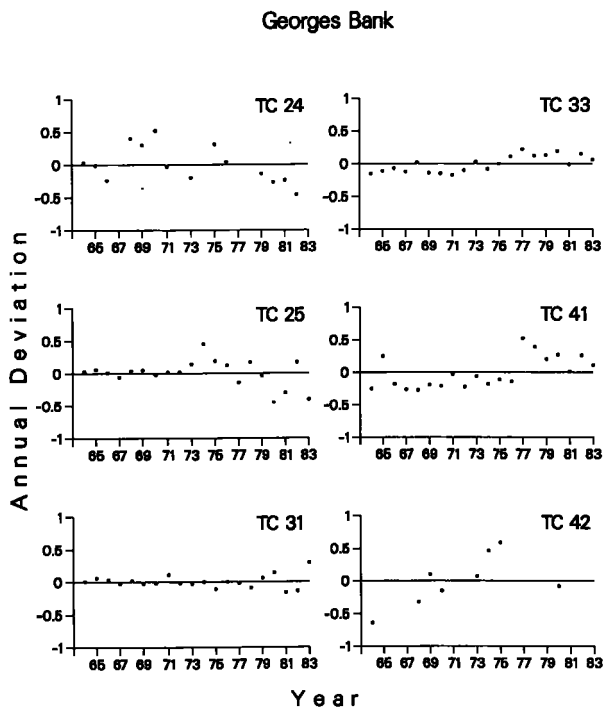

FIGURE 7.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Georges Bank.

class relative to a standard class vessel fishing for yellowtail flounder on and Cape Cod grounds, 1964–83.

Year	Vessel tonnage class[1]									
	21	22	23	24	25	31	32	33	41	42
				Southern New England						
1974	—	0.67	—	1.11	1.03	1.00		1.27	0.62	
1975	—	0.72	—	0.73	0.83	0.85		1.00	1.11	
1976	—	0.66	—	0.40	0.66	0.86		1.28	1.56	
1977	—	0.87	—	0.79	0.97	0.88		1.09	0.99	
1978	—	1.33	—	0.56	0.78	0.75		1.11	1.38	
1979	—	0.69	—	0.54	0.74	0.79		0.98	1.24	
1980	—	0.82	—	0.68	0.90	0.95		1.09	1.07	
1981	—	0.92	—	0.55	0.99	1.06		1.26	0.86	
1982	—	0.64	—	0.62	0.84	0.86		1.07	1.07	
1983	—	0.68	—	0.92	0.94	0.89		0.98	1.04	
				Cape Cod						
1964	—	0.62	0.52	0.73		1.08	1.04	—	—	
1965	—	0.67	0.55	0.73		1.65	0.98	0.96	—	
1966	0.44	0.42	0.48	0.58		1.42	0.69	—	—	
1967	—	0.32	0.36	0.64		1.30	0.79	1.07	—	
1968	—	0.44	0.37	0.71		1.55	0.91	0.99	0.43	
1969	—	0.60	0.48	0.73		1.31	0.89	—	—	
1970	—	0.44	0.45	1.01		1.56	[3]	[3]	1.25	
1971	—	0.57	0.93	1.19		1.10	0.93	1.20	1.65	
1972	0.93	0.88	0.63	1.09		1.09	0.79	0.97	1.05	
1973	0.51	0.66	0.53	0.94	1.00	0.95	0.96	0.82	1.43	
1974	0.40	0.55	0.43	0.76		0.83	0.87	0.90	0.66	
1975	0.40	0.59	0.64	0.74		0.75	0.85	0.57	0.62	
1976	0.18	0.68	0.72	0.88		0.73	0.80	0.97	1.12	
1977	0.14	0.42	0.61	0.74		0.71	0.70	1.08	1.26	
1978	—	0.40	0.75	0.90		0.93	0.73	0.91	2.84	
1979	0.47	0.43	0.68	0.87		1.06	0.83	1.06	1.48	
1980	0.12	0.27	0.60	0.80		1.03	0.95	1.01	1.53	
1981	0.31	0.34	0.52	0.75		1.07	0.54	0.83	1.34	
1982	0.27	0.35	0.60	0.88		1.19	0.77	0.96	1.17	
1983	0.36	0.79	0.64	1.02		0.68	0.80	0.77	0.43	

[2]Vessel classes 21, 22, and 23 combined on Southern New England grounds.

[3]Insufficient data for these categories.

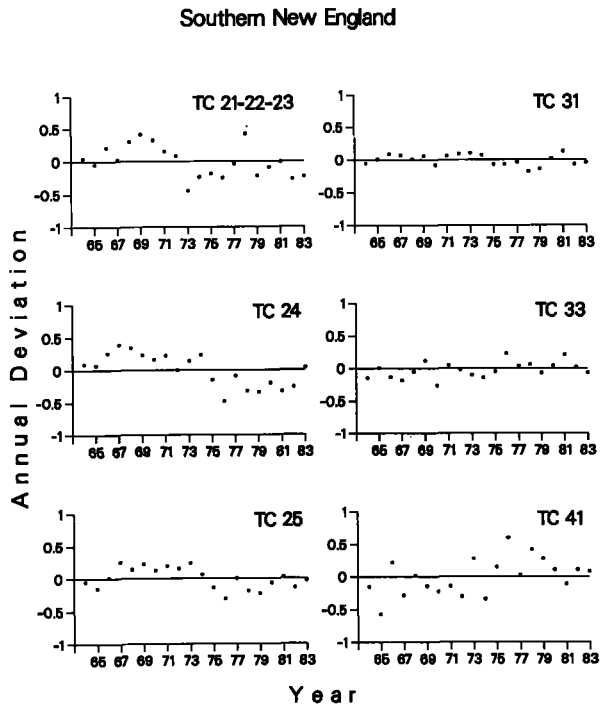

FIGURE 8.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Southern New England grounds.

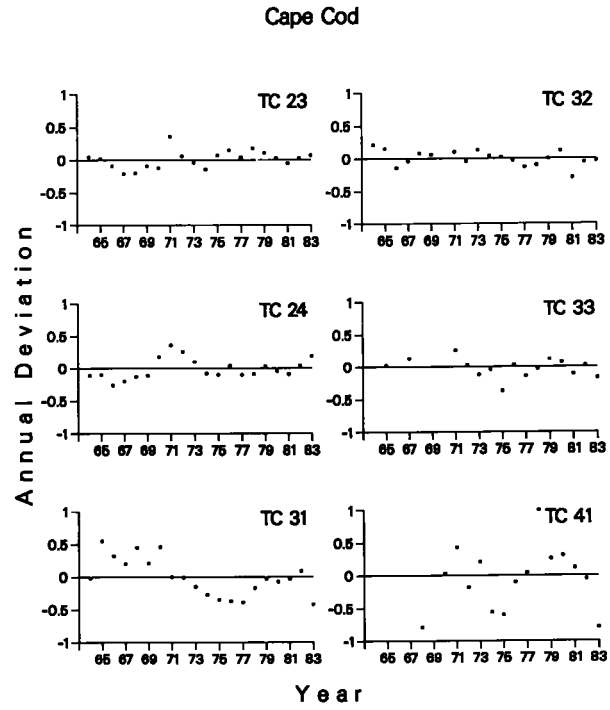

FIGURE 9.—Deviations in annual fishing power from the 1964–83 20-yr mean for major vessel tonnage classes fishing on Cape Cod grounds.

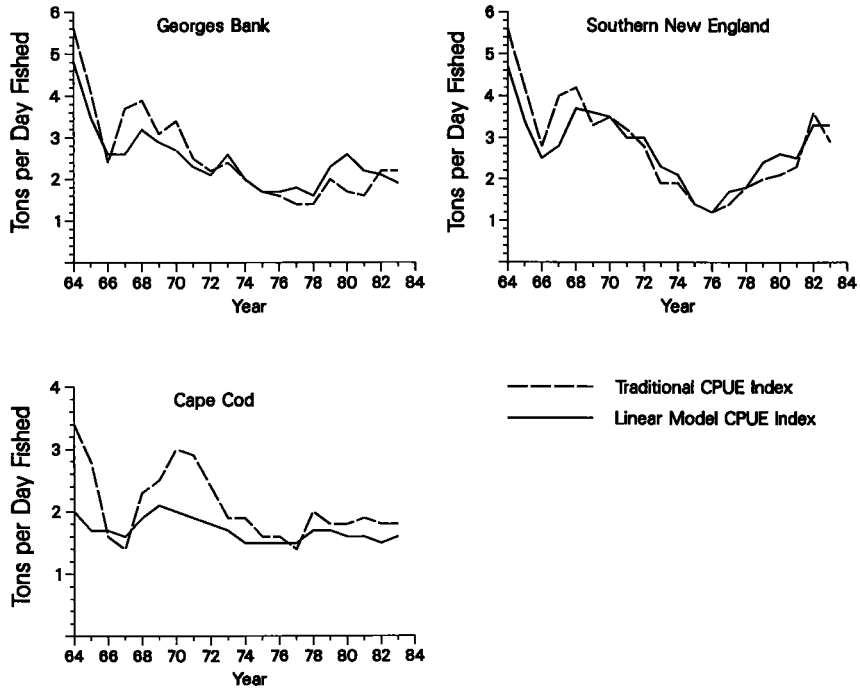

FIGURE 10.—Trends in annual yellowtail flounder CPUE (metric tons per day fished) calculated with traditional CPUE based on Lux (1964) and annual coefficients (linear model CPUE).

TABLE 6.—ANOVA results obtained from a three-way linear model incorporating year, quarter, and tonnage class for Georges Bank, Southern New England, and Cape Cod stocks of yellowtail flounder.

Source	df	Sum of squares	Mean square	F value	P
Georges Bank					
With interaction					
Model	211	1,432.92	6.79	29.53	<0.01
Year	19	908.42	47.81	207.88	<0.01
Qtr	3	107.36	35.79	155.59	<0.01
TC	9	84.24	9.36	40.70	<0.01
Yr*Tc	103	116.81	1.13	4.93	<0.01
Yr*Qtr	57	202.29	3.55	15.43	<0.01
Qtr*Tc	20	13.80	0.69	3.00	<0.01
Error	18,437	4,171.68	0.23		
Total	18,648	5,604.60	0.30		
Without interaction					
Model	31	1,100.02	35.48	147.83	<0.01
Year	19	908.42	47.81	199.21	<0.01
Qtr	3	107.36	35.79	149.11	<0.01
TC	9	84.24	9.36	39.00	<0.01
Error	18,617	4,504.58	0.24		
Total	18,648	5,604.60	0.30		
Southern New England					
With interaction					
Model	217	2,859.95	13.18	33.79	<0.01
Year	19	2,085.95	109.79	281.50	<0.01
Qtr	3	111.50	37.17	95.30	<0.01
TC	6	59.80	9.97	25.56	<0.01
Yr*Tc	114	257.12	2.26	5.78	<0.01
Yr*Qtr	57	304.89	5.35	13.72	<0.01
Qtr*Tc	18	40.69	2.26	5.80	<0.01
Error	26,879	10,612.21	0.39		
Total	27,096	13,472.16	0.50		
Without interaction					
Model	28	2,257.25	80.62	196.62	<0.01
Year	19	2,085.95	109.79	267.77	<0.01
Qtr	3	111.50	37.17	90.66	<0.01
TC	6	59.80	9.97	24.31	<0.01
Error	27,068	11,214.91	0.41		
Total	27,096	13,472.16	0.50		
Cape Cod					
With interaction					
Model	247	2,438.73	9.87	24.68	<0.01
Year	19	166.49	8.76	21.91	<0.01
Qtr	3	174.44	58.15	145.37	<0.01
TC	9	1,331.92	147.99	369.98	<0.01
Yr*Tc	135	526.18	3.90	9.74	<0.01
Yr*Qtr	57	167.62	2.94	7.35	<0.01
Qtr*Tc	24	72.09	3.00	7.51	<0.01
Error	19,097	7,731.24	0.40		
Total	19,344	10,169.97	0.53		
Without interaction					
Model	31	1,672.84	53.96	122.64	<0.01
Year	19	166.49	8.76	19.92	<0.01
Qtr	3	174.44	58.15	132.15	<0.01
TC	9	1,331.92	147.99	336.34	<0.01
Error	19,313	8,497.13	0.44		
Total	19,344	10,169.97	0.53		

TABLE 7.—Tonnage class, quarter, and year coefficients derived from a three-way linear model for the 1964–83 period for yellowtail flounder stocks on Georges Bank, Southern New England, and Cape Cod grounds.

	Georges Bank	Southern New England	Cape Cod
Tonnage class			
21	—	0.92	0.32
22	—	0.92	0.50
23	—	0.92	0.57
24	0.57	0.93	0.80
25	0.80	0.96	1.00
31	0.96	0.92	1.03
32	1.00	1.00	0.84
33	1.08	1.09	1.00
41	1.13	1.05	1.24
42	1.19	—	—
Quarter			
1	0.96	1.00	1.07
2	0.89	1.06	1.15
3	1.09	1.18	0.90
4	1.00	1.00	1.00
Year			
1964	1.00	1.00	1.00
1965	0.73	0.72	0.84
1966	0.55	0.54	0.84
1967	0.54	0.60	0.81
1968	0.68	0.79	0.93
1969	0.61	0.77	1.06
1970	0.58	0.75	1.00
1971	0.49	0.63	0.95
1972	0.45	0.65	0.88
1973	0.55	0.49	0.84
1974	0.42	0.45	0.77
1975	0.36	0.30	0.72
1976	0.37	0.25	0.76
1977	0.37	0.36	0.74
1978	0.34	0.39	0.83
1979	0.48	0.52	0.85
1980	0.55	0.56	0.78
1981	0.46	0.54	0.80
1982	0.44	0.71	0.77
1983	0.40	0.70	0.78

DISCUSSION

The analytical approach adopted in this paper is based on the hypothesis that CPUE of yellowtail flounder differs among the various tonnage classes of vessels and geographic regions associated with the fishery. In all of the analyses, the null hypothesis (i.e., no significant differences) was rejected only when the probability of obtaining a greater F statistic was <0.01. Even at this probability level, statistically significant results were often obtained when differences among variable levels appeared to be minimal due primarily to the large number of observations included in most analyses.

The initial series of ANOVAs, based on pooled CPUE data from all statistical areas encompass-

ing the three stocks, provided sufficient evidence to reject the null hypothesis. In each of the 20 years analyzed, the main effects of tonnage class and statistical area represented highly significant ($P < 0.01$) sources of variation. The tonnage class-area interaction term was also highly significant in all cases, implying that vessels of various tonnage classes exhibit different CPUE trends relative to each other in different areas.

The initial results established the basis for further investigations. In subsequent analyses, the data were grouped to test the null hypothesis that no significant differences in CPUE existed among the three traditionally accepted stock definitions (Georges Bank, Southern New England, and Cape Cod). The highly significant differences obtained in 19 out of 20 years indicate that catch rates differ among the three stocks. The resulting highly significant tonnage class-stock area interaction term obtained from the ANOVAs in all years suggests that standardization of CPUE among tonnage classes should be performed separately for each stock.

Analysis of variance within each stock provided the final basis for performing the standardized CPUE calculations. In these tests, the rejection of the null hypothesis for tonnage class main effects in all years for each stock suggests that separate fishing power coefficients must be calculated for each tonnage class even though the coefficients are similar in many cases. The ANOVA results also indicated that differences in CPUE among statistical areas within each stock were highly significant in 80% or more of the years implying that, within each stock region, yellowtail abundance is not homogeneous. This is not surprising since yellowtail flounder are prevalent only on certain grounds within each geographic region. Further analyses of the data by depth indicated no overall significant differences in CPUE between the two primary depth zones (1–55 m and 56–110 m) where yellowtail flounder are consistently caught.

The infrequent number of significant interactions on Georges Bank and Cape Cod grounds relative to Southern New England (Table 4) suggests a greater independence of the tonnage class and area main effects with respect to CPUE, i.e. both large and small vessels exhibited relatively similar changes in mean CPUE among statistical areas within each stock. In choosing data sets for computing fishing power coefficients we sought to minimize the amount of interaction among the vessel tonnage classes and geographic areas involved. This criterion was met to a greater extent for the Cape Cod and Georges Bank stocks than for the Southern New England stocks. It appears that yellowtail flounder inhabiting this region are subject to a more complex set of interactions perhaps due to temperature and bottom type. We decided, however, to accept the results for each of the three stocks and proceed with the calculations of fishing power coefficients.

Annual fishing power coefficients computed for each vessel tonnage class fishing on Georges Bank, Southern New England, and Cape Cod grounds provided a basis for examining the consistency in relative fishing power of individual tonnage classes over time. Annual deviations for Georges Bank and Southern New England grounds indicated a gradual change in relative fishing power of most tonnage classes between 1964 and 1983, and tests for autocorrelation of residuals indicated significant time effects. On these grounds, larger vessels exhibited higher catch rates relative to the standard in the later years as compared with the earlier years. Since many of the larger vessels have been replaced in recent years by newer vessels which are, presumably, equipped with more sophisticated electronics, any attempt to relate CPUE to stock abundance must account for such technological advances.

Similarly, changes in seasonal availability are often great enough to mask interannual variation in stock abundance. Thus, the presence of significant tonnage class-season interactions may be explained by the ability of certain vessel classes to effectively target seasonal concentrations. Since peak spawning of yellowtail flounder occurs during late spring (Lux 1964), the presence of high seasonal coefficients during the second and third quarters is not surprising.

By specifying the model to include tonnage class, annual, and seasonal components, we have attempted to account for technological and seasonal availability factors which interact with temporal changes in abundance. Although other factors could be incorporated in the model to account for a larger portion of the variation in CPUE, analyses of historical commercial fishing operations of this type are often limited to those attributes which can be directly linked to landings records (Kimura 1981; Westrheim and Foucher 1985). An alternate approach adopted by Stern and Hennemuth (1975) involved the use of a study fleet of selected vessels whose characteristics and fishing practices were closely monitored.

In our study, factors were selected for inclusion in the model based on prior knowledge of fleet characteristics and seasonal and spatial distribution patterns of the species. Despite this, the three attributes incorporated in the final model accounted for 15–25% of the total variation in CPUE, depending on the stock. Undoubtedly, other factors such as experience of the captain, net design and rigging, and variation in local fish abundance contribute substantially to overall variation in catch rates.

Differences between the annual CPUE estimates based on Lux's original fishing power coefficients and the recalculated indices occur in many cases because of shifts in the vessel composition of the fleet over the past 20 years. The inclusion of larger vessels in the more recent years, particularly on Georges Bank and Southern New England grounds, may account for the consistently higher CPUE estimates obtained for these areas since the mid-1970's. On Cape Cod grounds, CPUE estimates differ substantially prior to this time. Lux (1964) has stated that a relatively low proportion of the landings from this area were used in his CPUE computations and, consequently, the indices were not considered to be as valid a measure of relative abundance as those obtained for Georges Bank and Southern New England. Our analyses for Cape Cod grounds, based on data for the period since 1964, are subject to the same concerns since a large proportion of the yellowtail flounder landings continues to be taken incidentally.

Although the revised standardized CPUE estimates presented in this paper are based on a different standardization technique, trends are generally similar to those obtained previously. The revised procedure, however, accounts for seasonal and technological influences and insures complete representation of all vessel classes engaged in the yellowtail fishery.

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REDUCING THE BYCATCH IN A COMMERCIAL TROTLINE FISHERY

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ABSTRACT

Reducing the bycatch of red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*, in the Texas commercial trotline fishery is desirable. Hook placement within the water column was examined as a means of accomplishing this objective. The commercial trotline fishery was simulated in the Laguna Madre during February 1985 through January 1986. Requiring placement of trotline hooks on bottom will reduce bycatch of red drum, spotted seatrout, and other nonmarketable fishes and improve operational efficiency of commercial fishermen without significantly reducing catch of black drum, *Pogonias cromis*, a target commercial species. Other than crab and shrimp being more effective baits than oleander leaves, no other generalization could be made concerning baits and seasons.

Longlines catch species unwanted or legally nonretainable by fishermen and have been regulated to reduce the bycatch of nontargeted species (South Atlantic Fishery Management Council 1985). Trotlines (Figs. 1, 2) are a specialized longline used in shallow (<4 m) Texas estuaries to catch fish (Simmons and Breuer 1962; Breuer 1973, 1974, 1975; Matlock 1980). Red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus*, were the primary targets until 1981 when their sale was prohibited because of overfishing (Matlock et al. 1979; Anonymous 1979, 1981, 1983). The effort has since been redirected toward black drum, *Pogonias cromis*. Regulations requiring the use of circle hooks and placement of the mainline under water were enacted to reduce the bycatch of red drum and spotted seatrout. However, a bycatch still occurs. This study was conducted to determine if the bycatch could be further reduced by additional regulation of where in the water column hooks are fished and bait types.

MATERIALS AND METHODS

The catch on trotlines with hooks placed on the bottom or in the top of the water column was compared by simulating commercial fishing techniques in the Laguna Madre, TX (Fig. 3). Bottom trotlines were set with the mainline on the bottom. Top trotlines had the mainline floated with the hooks suspended in water ≥0.6 m deep to insure hooks fished in the water column. Texas Parks and Wildlife Department (TPWD) trotlines were set in the same area as commercial trotlines. Commercial fishermen were contacted by telephone within 24 hours prior to TPWD sets to determine areas of commercial activity. All TPWD trotlines were at least 15 m apart.

Trotlines with 100 hooks each were built according to commercial fishermen specifications (McEachron et al. 1985). The mainline (182.9 m long) consisted of #36 nylon twine, knotted twice every 1.8 m for swivel (1/0 black brass barrel) placement (Figs. 1, 2). Hooks (#8 Mustad 39960ST) were attached by a 610–686 mm long staging (56.7 kg test monofiliament) to the swivel at 1.8 m intervals. Stakes (51 cm × 76 mm) and/or anchors were placed on each end to stretch the mainline. Floats (3.8 L) were attached to the mainline every 15 hooks for navigation identification.

Eighteen trotlines were set overnight each month in both the upper and lower Laguna Madre during 1 February 1985 through 31 January 1986. Six (3 top; 3 bottom) were set during each of two monthly sampling periods (first and last 15 days of the month). Another six sets were made in either the first or last half of each month; the period was randomly selected each month. Each trotline was baited completely with one of three bait types—cut portions of blue crab, *Callinectes sapidus*; dead shrimp, *Penaeus* sp.; or oleander, *Nerium* sp. leaves—so that all bait types were used on both top and bottom trotlines during every period. These baits represented the most

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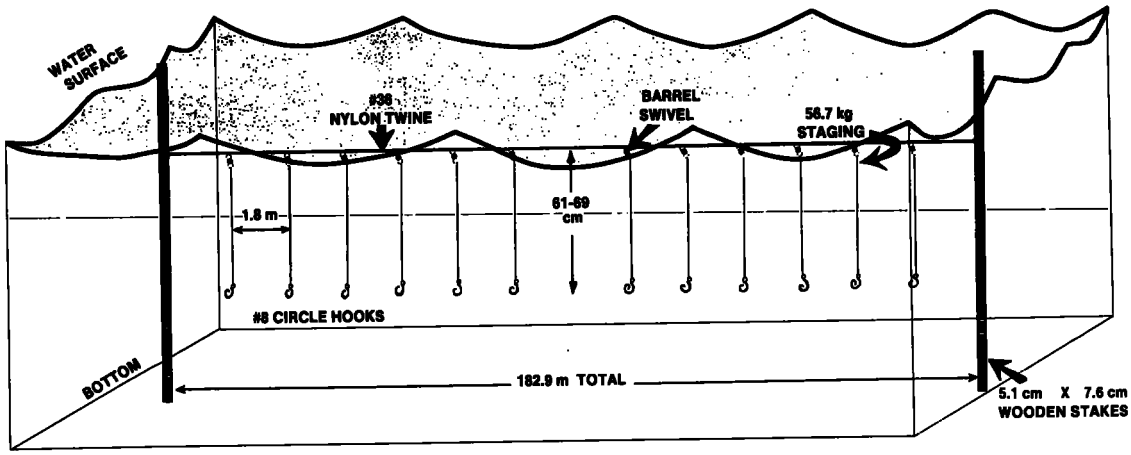

FIGURE 1.—Top trotline.

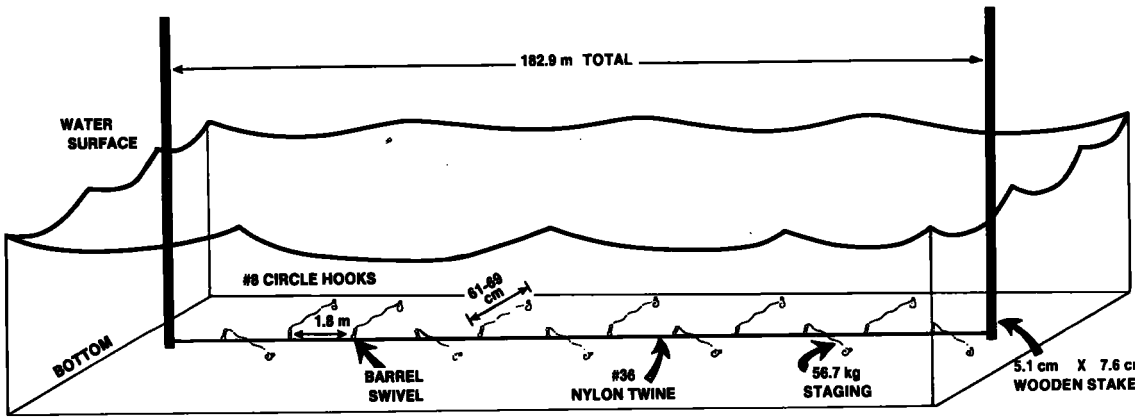

FIGURE 2.—Bottom trotline.

commonly used baits by commercial trotline fishermen (McEachron et al. 1980, 1986).

Fishes caught were identified (Hoese and Moore 1977; Robins et al. 1980), counted (Table 1), and total length (TL) was measured to the nearest 1 mm. Data were pooled into fall (September–November), winter (December–February), spring (March–May), and summer (June–August) to examine seasonal variation.

A catch rate (No./line · h) for black drum; red drum; spotted seatrout; hardhead catfish *Arius felis*; and total fishes was computed for each trotline set by dividing the number caught by the number of hours fished. Catch rates were transformed to log (catch rate + 1) and analyzed using a four-factor fixed-effects model analysis of variance (AOV). The four factors were 1) hook placement, at two levels—top and bottom; 2) bait, at three levels—crab, shimp, and leaves; 3) bay, at two levels—upper Laguna Madre and lower Laguna Madre; 4) season, at four levels—fall, winter, spring, and summer.

Differences in main effect means were evaluated with Ducan's multiple range test. However, when significant first-order interactions were found, comparisons were made within levels of the interacting factors using the mean square error (MSE) from the AOV.

Total lengths of each species were analyzed in a nested AOV to investigate differences among the four factors. However, because fish were not caught in all factor level combinations, factors and/or factor levels for each species were eliminated from analyses. Spotted seatrout lengths

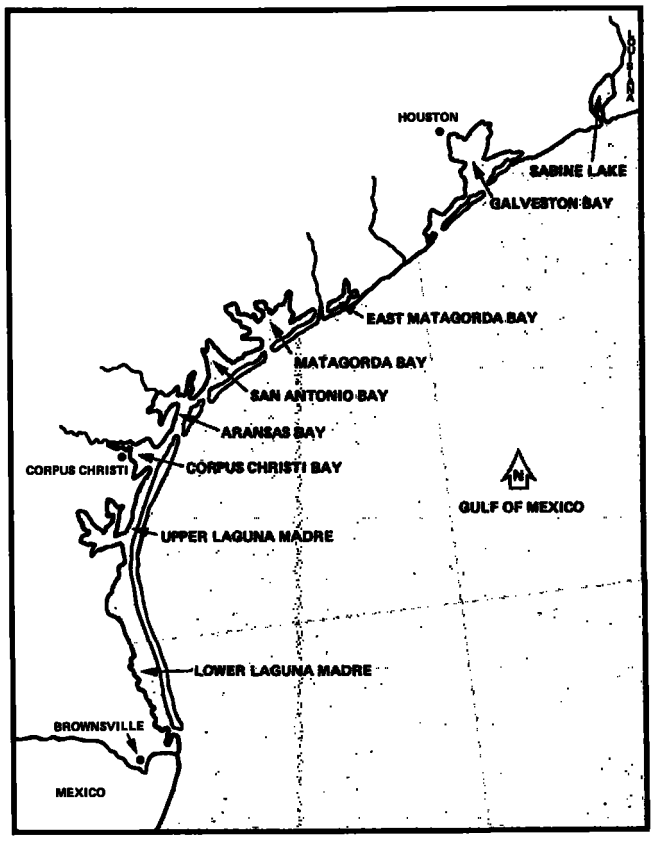

FIGURE 3.—Texas coast.

TABLE 1.—Number of fishes caught on trotlines in the upper and lower Laguna Madre during February 1985-January 1986.

Species	Upper Laguna Madre	Lower Laguna Madre	Total
Arius felis	977	1,652	2,629
Sciaenops ocellatus	352	658	1,010
Pogonias cromis	67	265	332
Cynoscion nebulosus	29	103	132
Micropogonias undulatus	36	51	87
Opsanus beta	34	1	35
Archosargus probatocephalus	1	24	25
Dasyatis americana	0	17	17
Dasyatis sabina	6	7	13
Elops saurus	4	4	8
Orthopristis chrysoptera	1	7	8
Bagre marinus	1	4	5
Lagodon rhomboides	0	5	5
Paralichthys lethostigma	1	3	4
Rhinoptera bonasus	0	4	4
Chilomycterus schoepfi	0	3	3
Ophichthus gomesi	3	0	3
Cynoscion arenarius	0	2	2
Negaprion brevirostris	0	1	1
Trachinotus carolinus	0	1	1
All species	1,512	2,812	4,324

were pooled for both bay systems because an insufficient number of spotted seatrout were caught for individual bay analyses. Factor levels eliminated from length analyses were leaves and winter from hardhead catfish, leaves and crab from spotted seatrout, and fall, spring, and summer from black drum. Spring and winter red drum lengths were pooled. Lower Laguna Madre data only were used for red drum, black drum, and hardhead catfish length analyses. Each measured fish length was an observational unit of a trotline set. Sets were a random factor nested within fixed main effect combinations. The nested set effect mean square was used for testing other effects when the set effect was significant. However, the AOV yields approximate F values because unequal numbers of fish were caught among sets.

SAS procedures (SAS Institute, Inc. 1980, 1982) were used for all analyses. The significance level for each AOV test was $\alpha = 0.01$ because the AOV used to examine catch rates of each species had 15 potential F tests. This alpha value assured that

the family level of significance would not exceed 0.15. All other tests were made with a significance level of $\alpha = 0.05$. Mean catch rates and confidence intervals computed from transformed data were back-transformed for tabular and graphic presentation (Elliott 1979).

RESULTS

Fishing trotlines on the bottom reduces bycatch without affecting catches of black drum, the target species. A significant difference could not be detected between black drum catch rates on top and bottom trotlines regardless of bait, season, or bay (Tables 2, 3). Catch rates for hardhead catfish, red drum, spotted seatrout and total fishes were significantly lower on bottom trotlines than on top trotlines (Tables 2, 3). Differences in catch rates between top and bottom trotlines for hardhead catfish, red drum, and total fishes did not vary significantly among seasons and baits but did vary between bays based on the first-order interactions (Tables 4, 5). A significant second-order interaction of position × bay × bait for spotted seatrout revealed that differences between top and bottom trotlines were affected by both bait and bay but not by season (Fig. 4).

No significant difference was found in red drum catch rates among baits nor in spotted seatrout catch rates among seasons (Tables 2, 3). All other main effects were significant for catch rates of all species and total fishes. Of the possible first-order interactions involving bait, season, and bay, only season × bait for hardhead catfish, red drum, and total fishes, bait × bay for black drum and total fishes, and season × bay for black drum, hardhead catfish, and total fishes were significant (Tables 4, 5). The second-order interaction of bait × bay × season for total fishes was significant (Fig. 5).

No significant differences were found in mean lengths of black drum, hardhead catfish, red drum, and spotted seatrout between top and bottom trotlines (Tables 6–8). Significant differences in mean length of hardhead catfish were detected for main effects of bait and season (Table 7).

DISCUSSION

Management objectives could be better met by requiring placement of trotline hooks on bottom than by allowing hooks to be fished from the surface. Red drum and spotted seatrout mortality would be reduced without significantly affecting

TABLE 2.—Mean back-transformed catch rate (No./line·h) and associated 95% confidence interval of black drum, hardhead catfish, red drum, spotted seatrout, and total fish caught on top and bottom trotlines by bait, bay, and season during February 1985-January 1986. Numbers in parentheses are the lower and upper values for the 95% confidence interval.

Species	Position[1]		Bait[2]			Bay[1]		Season[3]			
	Top	Bottom	Crab	Shrimp	Leaves	Upper Laguna Madre	Lower Laguna Madre	Fall	Winter	Spring	Summer
Black drum	0.049 (0.033-0.066)	0.039 (0.025-0.053)	0.072 (0.046-0.099)	0.044 (0.027-0.061)	0.017 (0.007-0.027)	0.017 (0.010-0.024)	0.071 (0.051-0.092)	0.019 (0.010-0.028)	0.113 (0.073-0.153)	0.037 (0.021-0.052)	0.010 (0.004-0.016)
Hardhead catfish	0.486 (0.411-0.566)	0.207 (0.165-0.249)	0.674 (0.563-0.793)	0.288 (0.233-0.345)	0.090 (0.055-0.126)	0.265 (0.216-0.316)	0.424 (0.355-0.498)	0.312 (0.246-0.381)	0.213 (0.136-0.295)	0.530 (0.418-0.651)	0.326 (0.250-0.407)
Red drum	0.209 (0.167-0.253)	0.047 (0.031-0.062)	0.123 (0.087-0.162)	0.155 (0.112-0.199)	0.103 (0.064-0.140)	0.089 (0.067-0.114)	0.166 (0.129-0.204)	0.072 (0.048-0.096)	0.299 (0.215-0.388)	0.062 (0.041-0.084)	0.084 (0.057-0.112)
Spotted seatrout	0.031 (0.022-0.041)	0.005 (0.001-0.009)	0.007 (0.003-0.011)	0.037 (0.023-0.051)	0.010 (0.004-0.016)	0.008 (0.003-0.012)	0.028 (0.019-0.038)	0.014 (0.007-0.022)	0.028 (0.014-0.042)	0.009 (0.004-0.015)	0.020 (0.008-0.033)
Total fish	0.839 (0.739-0.945)	0.319 (0.268-0.372)	0.925 (0.795-1.064)	0.578 (0.493-0.667)	0.234 (0.176-0.295)	0.408 (0.346-0.472)	0.745 (0.649-0.846)	0.452 (0.370-0.540)	0.717 (0.571-0.876)	0.677 (0.553-0.811)	0.460 (0.367-0.559)

[1] $N = 216$ for each species.
[2] $N = 144$ for each species.
[3] $N = 108$ for each species.

TABLE 3.—Summary of results of four-way AOV's of the mean transformed catch rate on top and bottom trotlines in the Laguna Madre during February 1985-January 1986.

Source of variation	df	Black drum			Red drum			Spotted seatrout			Hardhead catfish			Total		
		Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*	Sum of squares	*F*	*PR* > *F*
Total	431	0.9803			3.5951			0.2369			9.4078			12.3038		
Position	1	0.0015	0.82	0.37	0.2736	43.12	<0.01	0.0115	25.88	<0.01	0.5652	41.23	<0.01	1.7030	121.71	<0.01
Bait	2	0.0252	6.90	<0.01	0.0217	1.71	0.18	0.0113	12.68	<0.01	1.7919	65.36	<0.01	2.1632	77.30	<0.01
Season	3	0.0789	14.41	<0.01	0.2932	15.41	<0.01	0.0028	2.11	0.10	0.4590	11.16	<0.01	0.2515	5.99	<0.01
Bay system	1	0.0380	20.81	<0.01	0.0611	9.63	<0.01	0.0070	15.67	<0.01	0.1716	12.51	<0.01	0.6792	48.54	<0.01
Position × bait	2	0.0005	0.13	0.88	0.0091	0.72	0.49	0.0026	2.89	0.06	0.0380	1.39	0.25	0.0149	0.53	0.59
Position × season	3	0.0008	0.15	0.93	0.0664	3.49	0.02	0.0010	0.77	0.51	0.0393	0.96	0.41	0.0326	0.78	0.51
Position × bay systems	1	0.0006	0.33	0.57	0.0430	6.77	0.01	0.0118	26.60	<0.01	0.2229	16.26	<0.01	0.5231	37.38	<0.01
Bait × bay systems	2	0.0265	7.27	<0.01	0.0434	3.42	0.03	0.0012	1.40	0.25	0.0135	0.49	0.61	0.1366	4.88	0.01
Bait × season	6	0.0179	1.63	0.14	0.2014	5.29	<0.01	0.0050	1.86	0.09	0.3355	4.08	<0.01	0.4950	5.90	<0.01
Bay systems × season	3	0.0588	10.74	<0.01	0.0045	0.23	0.87	0.0011	0.82	0.48	0.2675	6.50	<0.01	0.4854	11.56	<0.01
Position × bait × bay systems	2	0.0004	0.13	0.87	0.0152	1.20	0.30	0.0050	5.66	<0.01	0.0026	0.10	0.91	0.0006	0.02	0.98
Position × bait × season	6	0.0018	0.16	0.99	0.0078	0.20	0.98	0.0008	0.30	0.94	0.0499	0.61	0.72	0.0390	0.46	0.83
Position × bay systems × season	3	0.0003	0.06	0.98	0.0153	0.80	0.49	0.0011	0.83	0.48	0.0720	1.75	0.16	0.0904	2.15	0.09
Bait × bay systems × season	6	0.0264	2.41	0.03	0.0806	2.12	0.05	0.0009	0.34	0.91	0.0761	0.93	0.48	0.2381	2.84	0.01
Position × bait × bay systems × season	6	0.0013	0.12	0.99	0.0227	0.60	0.73	0.0026	0.96	0.45	0.0384	0.47	0.83	0.0781	0.93	0.47
Error	384	0.7012			2.4363			0.1711			5.2641			5.3731		

TABLE 4.—Mean transformed catch rate of position × bay and bait × bay in significant two-way interactions. Means followed by the same letter in a row under a species heading are not significantly ($P > 0.05$) different.

	Position × bay				Bait × bay		
	Hardhead catfish		Red drum		Black drum		
Bay system	Top	Bottom	Top	Bottom	Crab	Shrimp	Leaves
Upper Laguna Madre	0.315 A	0.216 A	0.135 A	0.044 B	0.012 A	0.036 A	0.003 A
Lower Laguna Madre	0.665 A	0.197 B	0.286 A	0.050 B	0.133 A	0.052 B	0.031 B

TABLE 5.—Mean transformed catch rate of season × bait and season × bay in significant two-way interactions. Means followed by the same letter in a row under a species heading are not significantly ($P > 0.05$) different. ULM = upper Laguna Madre; LLM = Lower Laguna Madre.

	Season × bait						Season × bay			
	Hardhead catfish			Red drum			Black drum		Hardhead catfish	
Season	Crab	Shrimp	Leaves	Crab	Shrimp	Leaves	ULM	LLM	ULM	LLM
Fall	0.614 A	0.310 B	0.212 C	0.100 A	0.068 A	0.047 A	0.008 A	0.030 A	0.326 A	0.298 A
Winter	0.329 A	0.200 A	0.119 A	0.224 A	0.494 B	0.183 B	0.023 A	0.205 B	0.001 A	0.444 B
Spring	1.006 A	0.444 B	0.178 C	0.076 A	0.035 A	0.077 A	0.038 A	0.035 A	0.445 A	0.617 B
Summer	0.757 A	0.201 B	0.045 C	0.100 A	0.044 A	0.109 A	0.000 A	0.019 A	0.305 A	0.349 A

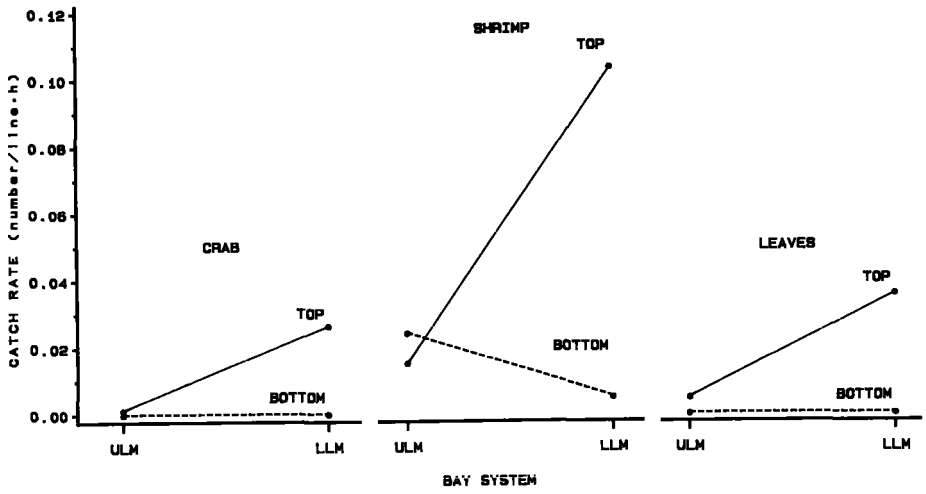

FIGURE 4.—Significant second-order interaction among positions, baits, and bay system for spotted seatrout catch rates. LLM = lower Laguna Madre, ULM = upper Laguna Madre.

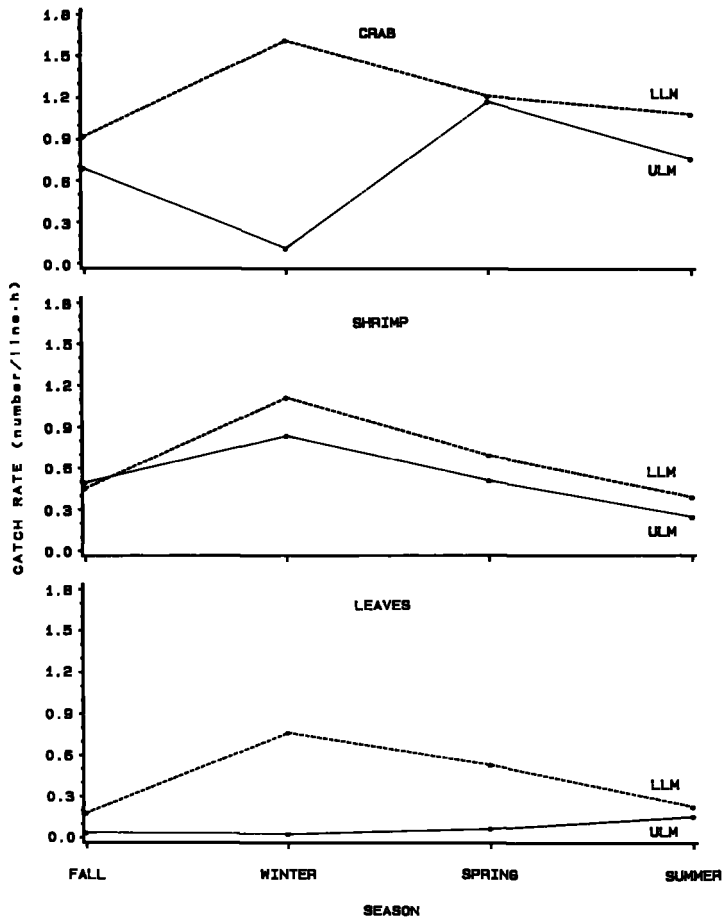

FIGURE 5.—Significant second-order interaction among bait types, bay system, and seasons for total fishes catch rates. LLM = lower Laguna Madre, ULM = upper Laguna Madre.

TABLE 6.—Mean length (mm ± 1SE) of black drum, hardhead catfish, red drum, and spotted seatrout caught on top and bottom trotlines by bait, bay and season during February 1985–January 1986. Number in parentheses is number of fish measured.

Species	Position		Bait		
	Top	Bottom	Crab	Shrimp	Leaves
Black drum	539 ± 10 (177)	550 ± 13 (146)	566 ± 11 (172)	493 ± 12 (108)	588 ± 21 (43)
Hardhead catfish	338 ± 1 (1,363)	343 ± 2 (675)	346 ± 1 (1,201)	328 ± 2 (651)	337 ± 3 (186)
Red drum	521 ± 4 (657)	504 ± 9 (173)	540 ± 6 (260)	481 ± 6 (336)	542 ± 7 (234)
Spotted seatrout	439 ± 9 (111)	420 ± 24 (18)	471 ± 23 (17)	426 ± 10 (86)	445 ± 19 (26)

Species	Bay		Season			
	Upper Laguna Madre	Lower Laguna Madre	Fall	Winter	Spring	Summer
Black drum	484 ± 19 (67)	560 ± 8 (256)	464 ± 20 (35)	538 ± 8 (201)	630 ± 21 (71)	416 ± 19 (16)
Hardhead catfish	327 ± 1 (824)	348 ± 1 (1,214)	329 ± 2 (538)	368 ± 2 (277)	333 ± 2 (724)	345 ± 2 (499)
Red drum	506 ± 7 (308)	523 ± 5 (522)	493 ± 11 (133)	506 ± 5 (427)	546 ± 9 (114)	551 ± 10 (146)
Spotted seatrout	411 ± 15 (29)	443 ± 10 (100)	410 ± 21 (25)	404 ± 12 (51)	482 ± 25 (16)	478 ± 13 (37)

TABLE 7.—Summary of results of the AOV's of mean length for black drum (winter season only), hardhead catfish (excludes leaves and winter season), and red drum (winter and spring seasons combined) on top and bottom trotlines in lower Laguna Madre during February 1985–January 1986. NA = not analyzed.

Source of variation	Black drum				Hardhead catfish				Red drum			
	df	Sum of squares	*F*	*PR > F*	df	Sum of squares	*F*	*PR > F*	df	Sum of squares	*F*	*PR > F*
Total	176	1,941,401			1,050	2,310,898			521	6,484,793		
Position	1	5,978	0.15	0.70	1	80	0.02	0.90	1	6,122	0.26	0.61
Bait	2	15,082	0.19	0.83	1	33,650	6.60	0.01	2	89,151	1.90	0.15
Season	NA				3	89,202	5.83	<0.01	2	133,190	2.85	0.06
Position × bait	2	49,063	0.69	0.55	1	8,242	1.62	0.21	2	10,913	0.23	0.79
Season × position	NA				3	1,517	0.10	0.96	2	789	0.02	0.98
Season × bait	NA				3	6,132	0.40	0.75	4	68,535	0.73	0.57
Season × position × bait	NA				3	10,269	0.67	0.57	4	63,388	0.68	0.61
Set (position × bait)	27	10,906,616	8.26	<0.01	NA				NA			
Set (season × position × bait)	NA				89	453,750	3.22	<0.01	91	2,129,491	2.61	<0.01
Error	144	704,611			946	1,499,474			413	3,706,235		

TABLE 8.—Summary of results of the AOV of mean length for spotted seatrout (shrimp bait only) on top and bottom trotlines in upper and lower Laguna Madre combined during February 1985–January 1986.

Source of variation	df	Sum of squares	*F*	*PR>F*
Total	85	750,362		
Position	1	601	0.04	0.84
Season	3	58,796	1.32	0.29
Position × season	3	58,462	1.31	0.29
Set (position × season)	28	416,855	3.42	<0.01
Error	50	217,744		

black drum catches. Operational efficiency of commercial fishermen should improve with less handling of nontarget species. Mortality of nontarget fishes would decrease because they would not be caught and subsequently handled. For red drum and spotted seatrout that are caught, survival would be high for those released back into the water. Survival of released red drum caught on trotlines in winter and summer and of spotted seatrout in winter was 100% (Martin et al. 1987). About 50% of the spotted seatrout died in summer cage studies; but few commercial trotlines are fished during this period (TPWD unpubl. data). Thus, the goal of reducing the catch of nontarget species and reducing mortality due to trotlines can be achieved with minimal impact on the commercial fishermen.

Interactions between bay system and the other three factors for some species probably reflect differences in relative abundance. Fewer fish were available to be caught in upper Laguna Madre than in lower Laguna Madre (Crowe et al. 1986). The effects of bait and season on trotline catches cannot be determined in bay systems where the fish abundance approaches zero.

No spotted seatrout were caught on crab bait on bottom in either bay; but they were caught on all baits on top in the lower Laguna Madre leading to the significant second-order interaction of position × bay × bait. This condition was not unexpected because spotted seatrout are predominately sight feeders (Vetter 1977), and might not take baits on bottom as readily as baits suspended in the water column.

Crab and shrimp were more effective baits than oleander leaves for all four species. No other generalizations could be made concerning baits and seasons. Selection of crab or shrimp as the bait of choice for reducing bycatch while maximizing black drum catch is unclear because catch rates for black drum and red drum were greater on crab than shrimp, especially in winter.

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LARVAL DEVELOPMENT OF BLUE GRENADIER, *MACRURONUS NOVAEZELANDIAE* (HECTOR), IN TASMANIAN WATERS

B. D. BRUCE[1]

ABSTRACT

The development of *Macruronus novaezelandiae* is described and illustrated from both reared specimens and larvae from Tasmanian waters. Eggs of *M. novaezelandiae* are pelagic, spherical (1.08–1.18 mm diameter), and have a single oil droplet (0.36–0.42 mm diameter). Eggs hatch after 55–60 hours at 14°–19°C. Larvae are 2.2–2.3 mm at hatching. Characteristic pigmentation, a myomere count of 78–80, and the sequence of fin development separate *M. novaezelandiae* from other known gadiform larvae. Development is direct, with no marked change in body morphology. Fin development proceeds in the sequence: second dorsal, anal, first dorsal, pelvic, caudal, pectoral. However, adult fin complements are reached in the sequence: first dorsal, pelvic, anal, second dorsal, caudal, pectoral.

Caudal development is late in *Macruronus*. Flexion begins at 20 mm and is not complete until 28 mm. The caudal fin is based on two ural centra, four hypurals, two epurals, and a parhypural. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores.

The genus *Macruronus* comprises four nominal species, which occur in southern temperate continental shelf and slope regions. Two species, *Macruronus novaezelandiae* and *M. magellanicus* support commercial fisheries. The blue grenadier, *M. novaezelandiae*, forms the basis of fisheries in New Zealand and Australia where total annual catches range up to 97,750 and 1,100 t respectively (Patchell 1982; Wilson 1981, 1982). *Macruronus magellanicus* is fished commercially off South America. The remaining species, *M. maderensis* and *M. capensis*, are known only from a limited number of specimens (Svetovidov 1948; Cohen 1986). Despite their economic importance and widespread distribution, very little is known of the early life history of any member of the genus. Patchell (1982) identified winter spawning grounds on the west coast of the South Island for New Zealand populations of *M. novaezelandiae* and similarly Wilson (1981, 1982) has suggested a winter spawning, on the west coast of Tasmania, for Australian *M. novaezelandiae*. This paper presents the first published information on the larvae of *Macruronus*.

In 1984, the Division of Fisheries Research of the Commonwealth Scientific and Industrial Research Organization established a multidisciplinary program to investigate the biology and ecology of blue grenadier in Tasmanian waters. An integral part of this program was a study of larval ecology. As such, it was first necessary to establish criteria for the identification of blue grenadier larvae. This paper describes the larval development of *M. novaezealandiae* from Tasmanian waters.

MATERIALS AND METHODS

Specimens were obtained from samples collected aboard the CSIRO Fisheries Research Vessel *Soela* between April 1984 and September 1985. Details of sampling strategies, locations, and procedures will be described in a subsequent manuscript. Larvae were obtained by sampling with a rectangular midwater trawl (RMT 1+8; Baker et al. 1973), a 1 m diameter ring net (500 μm mesh), and free-fall, vertical drop nets of 64 μm and 200 μm mesh (Heron 1982). Juvenile specimens were obtained with an Engels 352 pelagic trawl fitted with a 10 mm liner.

Newly hatched larvae were reared from eggs stripped and fertilized at sea. Eggs and milt stripped from ripe adults trawled from 500 m were mixed in 1 L plastic jars filled with seawater. Despite the jars being located in a seawater bath, incubation temperatures varied considerably (14°–19°C). On return to the laboratories at Hobart, the eggs were transferred to 2 L glass jars and placed in a constant temper-

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ature incubation chamber set at 14.0° ± 0.2°C. Incubation jars were not aerated, and no attempt was made to feed the larvae.

All specimens used for description were fixed in a 10% formalin-seawater solution buffered with sodium β-glycerophosphate and later transferred to a 5% solution.

This description is based on a series of 74 larvae, 2.2–34.2 mm in length, although comments on pigment and meristic variability stem from routine examination of several hundred specimens. A representative series of larvae is deposited with the South Australian Museum, Adelaide, South Australia.

Developmental terminology follows Ahlstrom et al. (1976). Body measurements follow Matarese et al. (1981). Length measurements are reported as notochord length, NL (i.e., from the snout tip to the end of the notochord) in preflexion and flexion larvae, and standard length, SL (i.e., from the snout tip to the posterior margin of the superior hypural elements) in postflexion larvae and juveniles. Larvae were measured under a dissecting microscope fitted with an ocular micrometer and a camera lucida. Juveniles were measured with vernier calipers.

Meristic counts and examination of ossification sequences were made on specimens cleared and stained using Alizarin Red S-KOH-glycerine (Hollister 1934). Caudal osteology follows Inada (1981), Marshall and Cohen (1973), and Monod (1968).

Vertebral counts include the first vertebrae, the neural spine of which is fused to the supraoccipital crest (Marshall 1966), and both ural centra. Vertebral centra were counted as ossified only when a complete band of stain connected both neural and haemal spines.

RESULTS

Identification of *M. novaezelandiae* larvae was based on their typical gadiform morphology (large head, compact gut, tapering body form), myomere count, and the development of confluent dorsal-caudal-anal fins (see section on Distinguishing Features). Identification of field-collected specimens was confirmed by comparison with reared larvae.

Distinguishing Features

Prior to median fin development, myomere counts are useful in separating *M. novaezelandiae* larvae (78–80) from similarly pigmented morid (41–72), macrourid (10–16 + 70 > 100), gadid (39–64) and other known merlucciid larvae (48–58) which they superficially resemble (Marshall and Iwamoto 1973; Fahay and Markle 1984; present study).

Both *M. novaezelandiae* and most morid larvae show moderately pedunculate pectoral fins, a feature common in gadiform larvae with delayed caudal development (Fahay and Markle 1984). Macrourid larvae, in contrast, have very prominently stalked pectorals and can further be separated from *M. novaezealandiae* and most morids by precocious development of the pelvic fin.

Size at caudal flexion and the sequence of fin development are also useful in separating *M. novaezelandiae* from all *Merluccius* species. In *Merluccius*, notochord flexion generally begins at about 9 mm and the caudal fin is the first to form (Dunn and Matarese 1984; Fahay and Markle 1984). *Macruronus novaezelandiae* larvae do not begin caudal flexion until approximately 20 mm, and the caudal fin is the second last to form.

Macruronus novaezelandiae larvae have 1–3 prominent melanophores along the ventral midline of the tail (although variable in appearance, see section on Trunk and Tail Pigmentation) and a double series of dorsal melanophores. When expanded, melanophores in these two regions coalesce to give the appearance of a broad postanal band. Postanal banding patterns are widespread in gadoid larvae (Fahay and Markle 1984); however, unlike many gadoid larvae, *M. novaezelandiae* lacks pigment at the notochord tip.

At larger sizes *M. novaezelandiae* larvae develop long-based dorsal and anal fins confluent with the caudal fin. Other gadoid larvae with this configuration have markedly different pigmentation (see Fahay and Markle 1984 for details). Ophidiiform larvae have confluent dorsal, caudal, and anal fins but can be separated from *M. novaezelandiae* by their lack of a separate first dorsal fin and general lack of body pigment (see Gordon et al. 1984).

Development

Embryonic development has not been treated in detail here as it is the subject of a manuscript in preparation by G. Patchell (Fisheries Research Centre, Wellington, New Zealand).

The pelagic eggs of blue grenadier are spherical, with an unsegmented yolk and a smooth cho-

rion. Late-stage eggs are 1.08–1.18 mm in diameter with a single oil droplet of 0.36–0.42 mm diameter (Fig. 1A). Reared larvae hatch at 2.2–2.3 mm after 55–60 hours (14°–19°C). Newly hatched larvae have a posteriorly positioned oil droplet and adopt a head down position in rearing containers. Yolk absorption was incomplete in specimens reared to 3.7 mm (6 days posthatch), although the smallest field-collected larvae (3.6 mm) had already completed yolk absorption. The anus opened laterally to the right in all reared larvae and 95% of field-collected larvae. The anus becomes symmetrical by 5.1 mm. A lateral anal opening in *M. novaezelandiae* is consistent with the developmental pattern reported for other gadiform species (Marak 1967; Matarese et al. 1981; Fahay and Markle 1984; Dunn and Vinter 1984).

Field-collected larvae are moderately elongate with the greatest body depth (16–22% body length) occurring at or near the pectoral fin base (Table 1). Head length as a proportion of body length (BL) remains relatively constant at about 22% BL throughout the larval phase, decreasing to about 17% BL in juveniles. Eye diameter decreases from 9% BL in preflexion larvae to 4% BL in juveniles. Depth at anus remains relatively constant at about 13% BL in larvae and juveniles. Distances from the snout tip to the first dorsal fin and from the snout tip to the anal fin decrease slightly during development from about 27% BL to 21% BL and 51% BL to 46% BL respectively.

in the number of melanophores and their degree of expansion. Although Badcock and Merrett (1976) suggested the appearance of melanophores can change on a diurnal rhythm, in the blue grenadier larvae examined, there was no conspicuous relationship between time caught and melanophore expansion.

Head Pigmentation

Newly hatched larvae (2.2–2.3 mm) have melanophores concentrated in front and behind the eye (Fig. 1B). Melanophores increase in number and extend over the sides of the head and snout by 3.3–3.5 mm (reared larvae, Fig. 1C). Melanophores migrate dorsally to the top of the head by 3.6 mm (Fig. 1D). Eyes become pigmented at this size in reared larvae. By 4.5 mm, the dorsal pigment on the head consists of a group of 3–11 melanophores scattered over the hindbrain and posteriorly to above the cleithrum. Pigment gradually extends over the midbrain, with 1 or 2 melanophores usually present between the eyes by 5.3 mm. Melanophores develop externally over these initial mid- and hindbrain spots and extend posteriorly as a double row to the dorsal fin anlage by 7.2 mm. Dorsal pigment gradually intensifies: melanophores increase in number and form a cap over mid- and hindbrains by 16.0 mm. Melanophores extend down between the eyes to the tip of the maxilla by 12.0 mm. Internal

TABLE 1.—Body proportions of larvae and juveniles of *Macruronus novaezelandiae* (expressed as percentage NL or SL): mean, standard deviation, range.

Body proportions	Preflexion			Flexion			Postflexion			Juvenile		
sample size	42			4			4			2		
	X	SD	range	*X*	SD	range	*X*	SD	range	*X*	SD	range
length (mm)	8.9	4.5	(3.6–19.0)	23.5	2.3	(20.6–26.1)	30.0	2.9	(27.6–34.2)	189.0	1.4	(188.0–190.0)
head length	22.7	1.7	(18.3–24.7)	23.7	1.0	(22.3–24.7)	22.3	1.4	(20.5–23.6)	17.6	0.4	(17.3–17.9)
eye diameter	9.2	0.7	(8.1–10.3)	7.9	0.4	(7.3–8.3)	7.3	0.7	(6.5–8.0)	4.2	0.4	(4.4–5.2)
snout length	6.1	0.9	(4.6–7.7)	6.2	0.6	(5.7–7.0)	5.9	0.5	(5.4–6.5)	4.9	0.1	(4.8–5.0)
depth at pectoral	22.3	1.7	(21.0–24.4)	17.9	0.6	(17.2–18.5)	16.6	2.0	(13.7–18.5)	13.1	0.1	(13.0–13.2)
depth at anus	12.0	2.4	(8.2–15.2)	13.1	0.3	(12.6–13.4)	13.0	0.8	(12.3–13.8)	12.7	0.6	(12.3–13.1)
snout to first dorsal fin	27.5	1.3	(25.2–29.3)	26.6	0.8	(26.0–27.7)	25.3	0.8	(24.2–26.0)	20.7	0.2	(20.6–20.9)
snout to anal fin	51.4	0.9	(50.0–52.6)	50.4	0.5	(49.6–50.6)	46.6	1.5	(45.0–48.4)	46.5	1.2	(45.7–47.4)

Pigmentation

Although pigmentation in *M. novaezelandiae* is variable, certain features persist that, when combined with meristic and morphometric information, enable identification. Variation in the appearance of pigmentation is a result of differences

pigment expands over the forebrain in larvae from 9.0 to 15.0 mm.

Ventral pigment on the head first develops in 4.2 mm larvae as 3–5 melanophores between the dentaries. The number of melanophores increases to 10–12 by 12.0 mm.

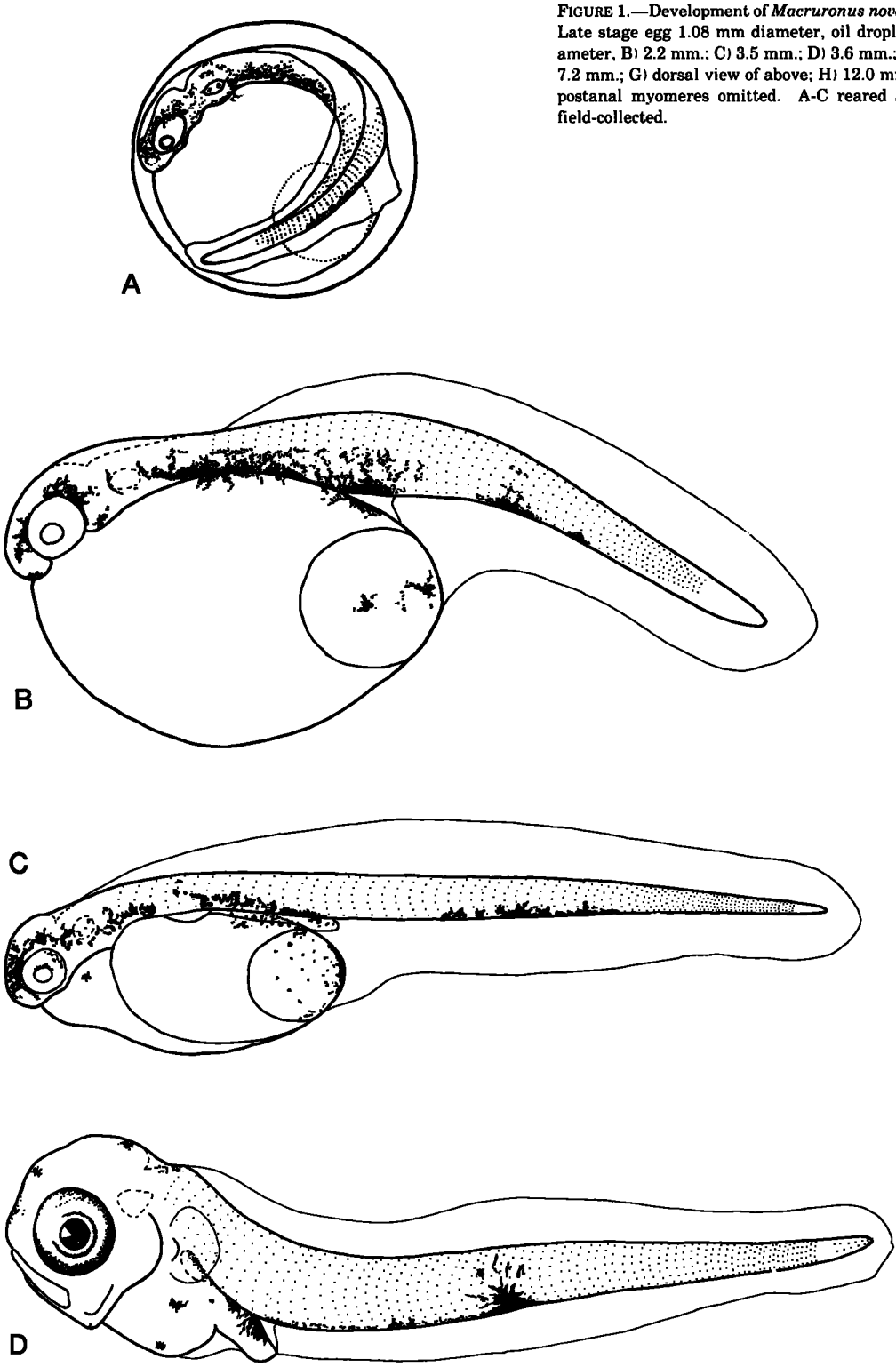
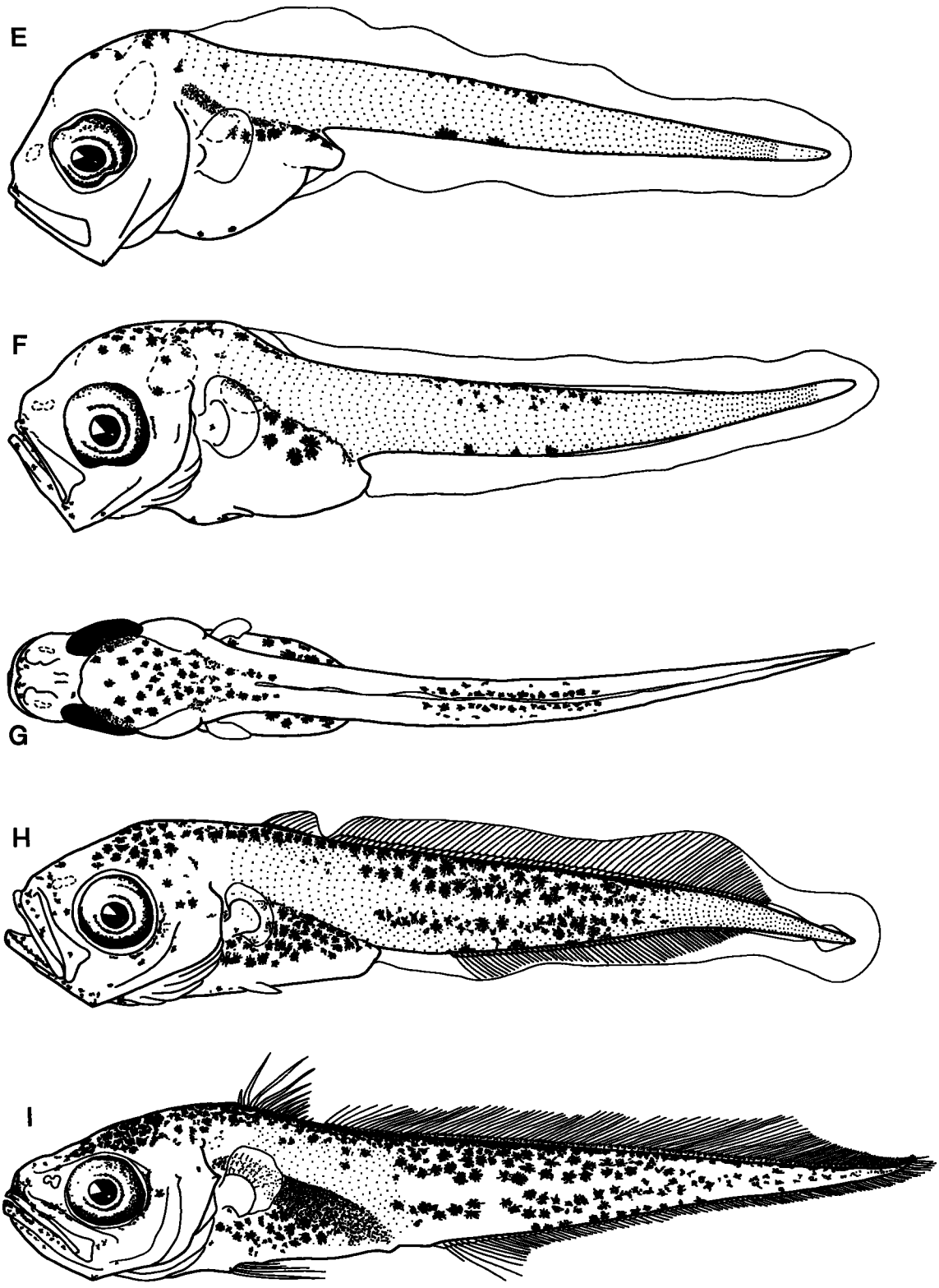


FIGURE 1.—Development of *Macruronus novaezelandiae:* A) Late stage egg 1.08 mm diameter, oil droplet 0.37 mm diameter, B) 2.2 mm.; C) 3.5 mm.; D) 3.6 mm.; E) 5.3 mm.; F) 7.2 mm.; G) dorsal view of above; H) 12.0 mm.; I) 24.2 mm. postanal myomeres omitted. A-C reared specimens, D-I field-collected.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The onset of dentary pigment is variable; no pigment may be present on some larvae as large as 7.0 mm. Most larvae develop 1 or 2 melanophores over the posterior section of the dentary by 5.3 mm and add melanophores anteriorly along its length, with 5 or 6 usually present by 7.1 mm.

Two melanophores are often present around the otic capsule by 7.0 mm, but they are obscured by overlying tissue in 10.0 mm larvae. Scattered melanophores develop over the pterotic region by 25.0 mm, but the operculum and preoperculum remain largely unpigmented, even in the largest specimen examined (34.2 mm).

Trunk and Tail Pigmentation

Newly hatched larvae have melanophores on the body above the yolk sac and ventrally on the tail. Some pigment is also present on the yolk sac near the developing gut and scattered over the oil droplet. Pigment forms a cap over the gas bladder by 4.2 mm. Melanophores are gradually added to the lateral surfaces of the gut throughout the larval period until the entire gut (including the ventral surface) becomes pigmented by 30.0 mm.

Dorsal pigment first appears on larvae 3.8–4.5 mm as scattered melanophores at approximately 60% NL. Melanophores rapidly increase in number and form a double row, extending from 51% to 67% NL in larvae of 5.0 mm. Lateral melanophores may also develop above the body midline in this region. Concurrently, a similar double row of melanophores appears and extends posteriorly from the head (Fig. 1G). The head and tail rows join by 10.5 mm. Melanophores appear posteriorly in the caudal region by 29.0 mm forming a twin series one either side of the developing dorsal fin. Pigment also appears internally on the dorsal surface of the vertebrae in larvae of 9.5 mm and extends anteriorly to approximately 50% SL and posteriorly to the last vertebrae by 34.0 mm.

Single melanophores appear on the dorsal fin ray bases by 14.0 mm and are present on all bases by 29.0 mm.

Pigment along the ventral midline of the tail appears in newly hatched larvae as a diffuse region that extends posteriorly from the yolk sac to 75–82% NL. This contracts to 1–3 melanophores (most commonly 2) located 52–65% NL in larvae of 3.8–4.0 mm. Additional melanophores (up to 6) may appear later, but the initial 1–3 melanophores persist throughout the larval period. In larvae larger than 7.0 mm, the initial 1–3 melanophores appear internally above the anal fin ray bases and are gradually obscured by both overlying musculature and external melanophores. These ventral melanophores on the tail are a useful diagnostic character, although their appearance varies, depending on their degree of expansion. This variability in melanophore appearance is particularly evident in small larvae where expanded ventral melanophores may extend over the lateral surfaces of the body to almost the dorsal area (Figs. 1D, 2).

Lateral pigment gradually intensifies throughout the larval period, excepting the area immediately above the gut, which remains largely devoid of pigment even in the largest specimen (34.2 mm).

Morphological Variability

Macruronus novaezelandiae larvae showed some size variation in development. In general, specimens captured in ring net and RMT samples appeared to develop features at slightly smaller sizes than those taken from drop net samples. This is likely a result of differential shrinkage of specimens caught by the different capture systems. Hay (1981) reported that considerably more shrinkage occurred in Pacific herring when larvae were killed prior to fixation and that shrinkage increased with tow length. Ring net and RMT tows varied in duration from 15 to 110 minutes, with most larvae dead by the time the net was retrieved and the catch fixed. Drop net sampling, in contrast, lasted for, at most, 3 minutes duration, and many larvae were still alive on fixation. Some variability in development can also be expected in field-collected larvae as a reflection of past history (e.g., feeding success), although it is unlikely such variations would account for the observed differences between larvae caught by different techniques.

Meristics and Osteology (Table 2)

Head and Axial Skeleton

In laboratory-reared larvae, jaw development was first visible after 3.5 days (posthatch) with a functional mouth present in larvae of 5.5 days (3.7 mm). Pigmentation of the eyes also occurred at this time suggesting that larvae were ready for first feeding. The smallest larva stained was a field-collected specimen 3.7 mm NL. The maxilla, premaxilla, dentary, and cleithrum were all ossified in this specimen.

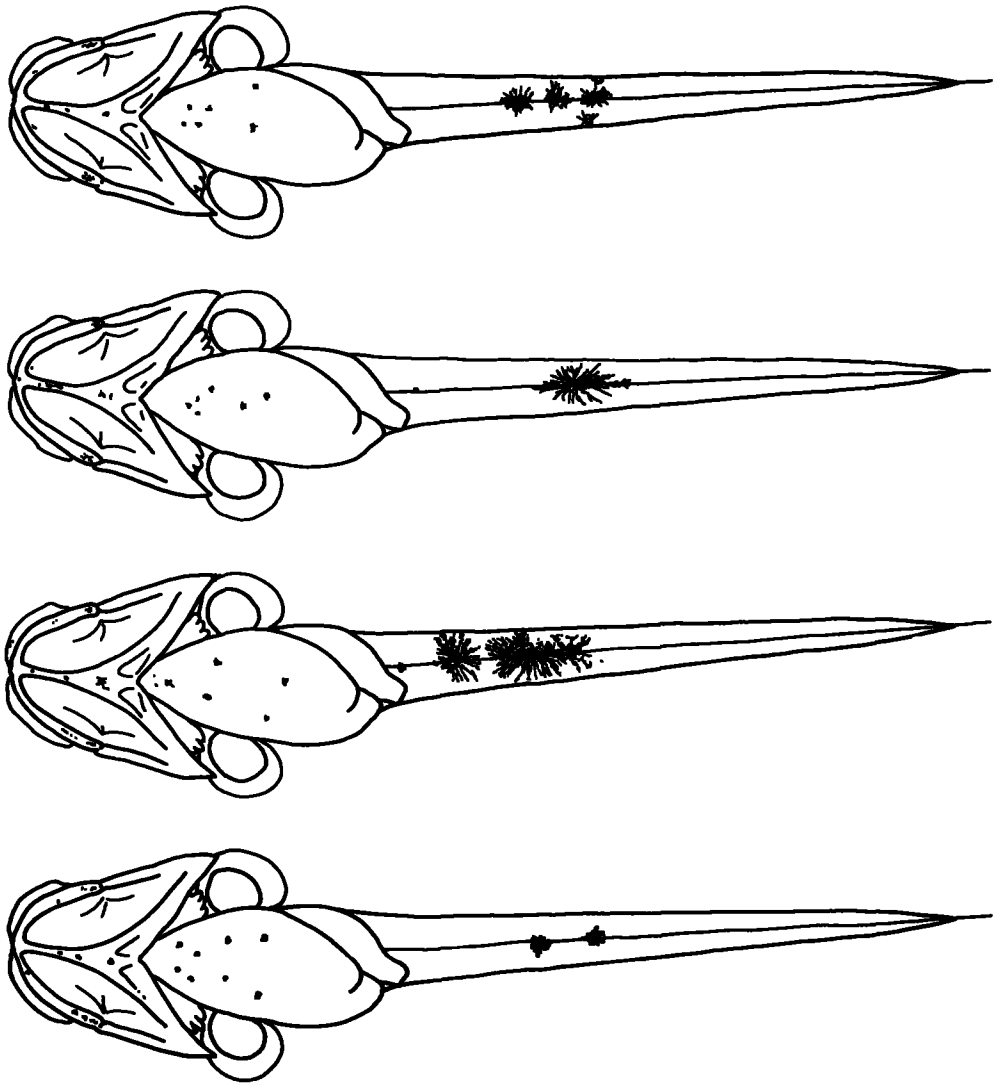

FIGURE 2.—Variability of ventral pigment on the tail in 4.9 mm larvae of *Macruronus novaezelandiae*.

Ossification of branchiostegals begins in larvae of 4.6 mm, with the full complement of 7 ossified by 11.5 mm. Gill rakers are first discernible in larvae of 9.4–9.9 mm with the full complement of 7 + 22 – 23 present by 28.9 mm.

Ossification of neural and haemal spines generally precedes that of the vertebral centra. Ossification of centra, neural spines, and haemal spines occurs sequentially from anterior to posterior proceeding slowly in larvae less than 9.0 mm in length and then more rapidly until the full complement is ossified by 23.2 mm. Elements associated with the caudal complex are the last to ossify.

Fins

Completion of fin development in *M. novaezelandiae* occurs in the sequence: first dorsal and pelvic (almost simultaneously), anal, second dorsal, caudal, pectoral.

Pelvic fins first appear in larvae of 5.7–5.8 mm as slight swellings either side of the gut. They do not form distinct buds until 6.9 mm. Ossification

TABLE 2.—Meristic counts from cleared and stained larval and juvenile *Macruronus novaezelandiae*. Specimens between dashed lines are undergoing notochord flexion. a = specimen damaged; b = juveniles not stained.

Length (mm)	Fin rays				Branchiostegal rays	Gill rakers			Total centra	Neural spines	Haemal spines	Caudal elements
	dorsal	anal	pectoral	pelvic		upper	lower	total				
3.7	—	—	—	—	—	—	—	—	—	—	—	—
3.9	—	—	—	—	—	—	—	—	—	1	—	—
4.2	—	—	—	—	—	—	—	—	—	1	—	—
4.6	—	—	—	—	1	—	—	—	—	2	—	—
4.8	—	—	—	—	1	—	—	—	—	2	—	—
5.2	—	—	—	—	3	—	—	—	—	2	—	—
6.0	—	—	—	—	3	—	—	—	—	3	—	—
7.4	—	—	—	—	5	—	—	—	5	6	—	—
9.4	4 + 28	18	—	3	6	—	8	8	42	55	37	—
9.9	0 + 19	4	—	—	6	—	6	6	38	54	34	—
11.5	9 + 74	60	—	4	7	—	12	12	55	58	42	—
16.3	12 + 84	73	4	8	7	1	15	16	70	70	55	3
17.4	12 + 86	76	4	8	7	3	15	18	71	70	55	3
19.8	13 + 87	86	3	8	7	5	15	20	73	74	57	4
23.2	12 + 100	90	9	8	7	5	17	22	76	74	57	5
26.1	13 + 99	90	13	8	7	5	21	26	76	74	57	5
28.9	13 + 99	91	9	8	7	7	22	29	78	76	57	a
188	13 + 94	90	20	8	7	7	22	29	b	b	b	b
190	13 + 96	90	20	8	7	7	23	30	b	b	b	b

may start as early as 9.4 mm with the full complement (8 rays) present by 16.3 mm. Ossification proceeds from the outer to the innermost rays.

The second dorsal fin anlage is visible in larvae of 5.7 mm. Bases are first visible by 6.9 mm, with ray ossification commencing by 7.3 mm. Although the anal fin anlage does not form until 6.9 mm, complete ossification is reached before that of the second dorsal. Distinct anal fin bases are first visible in 7.2 mm larvae and ossification has consistently begun by 9.9 mm. The full complement of anal rays is present by 21.0 mm and for the second dorsal, by 23.2 mm.

The first dorsal starts development slightly later than the second dorsal, although it is the first fin to complete ossification. The full complement of 12 or 13 elements is present by 16.3 mm.

Pectoral buds were first observed in larvae 4.5 days posthatch (3.2 mm). However, the pectoral fin is the last to complete development. Ossification of pectoral rays starts by 16.3 mm; a 34.2 mm specimen had only 15 ossified rays, still short of the 20 rays of juveniles. Sequence of ossification is from upper to lower.

The caudal fin anlage first appears on the ventral surface of the notochord just anterior to the tip in larvae of 10.4 mm. Flexion begins at 20 mm and is usually complete by 28 mm. Ossification of all caudal elements was incomplete in a 34.2 mm specimen. Insufficient material of the appropriate size was available to define the completion of caudal ossification.

The caudal complex in *M. novaezelandiae* is based on two ural centra, two epurals, a superior hypural (HP3 + 4), inferior hypural (HP1 + 2), and a parhypural (Fig. 3). Eight to nine rays articulate with these elements—one or two rays on the second epural, three rays on the superior hypural, two on the inferior hypural, and one ray each on the first epural and the parhypural. Single rays also articulate with the elongate neural and haemal spines of the first preural centrum. X and Y bones are present although they are not readily distinguishable from dorsal and anal pterygiophores. Total caudal fin ray counts are low (12 or 13).

Additional caudal structures occurred in one of the six specimens examined. This specimen had a twin haemal spine on the first preural centrum and greatly elongated haemal spines on preural centra 3–8 (1.3–1.4 times the length of corresponding neural spines, Fig. 3).

DISCUSSION

The general morphology and pigmentation of *M. novaezelandiae* larvae show broad similarities to *Merluccius* and to gadine gadids. Characteristic differences between *M. novaezelandiae* and *Merluccius* species occur in fin structure and the sequence of fin development. In *Merluccius*, the caudal fin is the first to form, followed by the pelvic. In *Macruronus*, caudal development is late with the caudal fin being the second last to

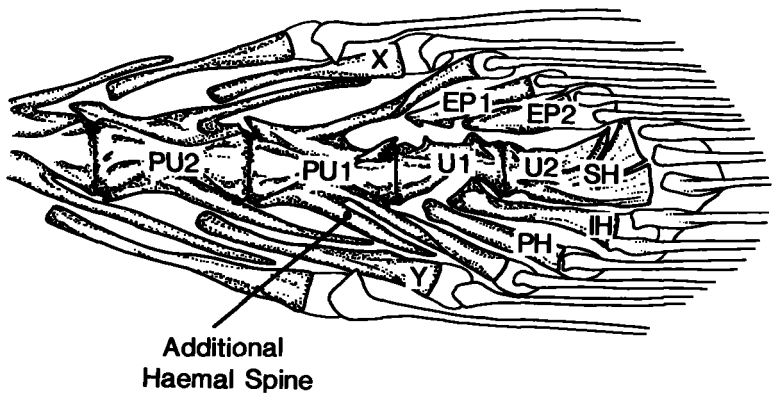

FIGURE 3.—Caudal osteology of a juvenile *Macruronus novaezelandiae* (181 mm SL). X = X bone, Y = Y bone, EP = epural, SH = superior hypural (hypurals 3+4), IH = inferior hypural (hypurals 1+2), PH = parhypural, U = ural centra, PU = preural centra.

form. The pectoral fin in *Macruronus* larvae is more markedly stalked than in *Merluccius*. Fahay and Markle (1984) suggested that this pectoral modification in larvae with delayed caudal development may be a compensatory response associated with swimming.

Although the larvae of the remaining merlucciid genera (*Lyconus* and *Lyconodes*) are currently unknown, fin structure and position should be useful in separating these from *Macruronus*. Based on adult features, pelvic insertion should distinguish *Macruronus* (pelvics inserted behind pectorals) from *Lyconus* (opposite) and *Lyconodes* (abdominal). Additionally, *Lyconus* has only a single dorsal fin and no caudal fin.

The caudal fin of *M. novaezelandiae* is similar to *Muraenolepis* in its confluence with dorsal and anal fins (Fahay and Markle 1984). This similarity extends to the undifferentiated X and Y bones and the total caudal fin ray count (12 or 13) reported by these authors. However, unlike *Muraenolepis*, *M. novaezelandiae* has radials fused to the spines of the first preural centrum, which is the more typical gadoid condition.

Variability in the structure and appearance of bones associated with the caudal fin has been reported for other *Macruronus* species. Marshall (1966) observed double neural arches and "supernumary elements" in *M. magellanicus*. Indeed, variability in gadiform caudal structure appears not to be unusual with examples in several taxa (Markle 1982). Unfortunately, insufficient specimens in the appropriate 35–150 mm size range were available to assess developmental characteristics of these variations in blue grenadier.

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NOTE: Since the acceptance of this paper, the embryological work by A. Patchell (see section on Development) has been published in New Zealand Journal of Marine and Freshwater Research Vol. 21, No. 2. That paper includes a similar larval developmental sequence to that reported here.

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THE DISTRIBUTION, ABUNDANCE, AND TRANSPORT OF LARVAL SCIAENIDS COLLECTED DURING WINTER AND EARLY SPRING FROM THE CONTINENTAL SHELF WATERS OFF WEST LOUISIANA[1]

JAMES H. COWAN, JR.[2] AND RICHARD F. SHAW[3]

ABSTRACT

The larvae of six species of Sciaenidae were collected in continental shelf waters off west Louisiana on five midmonthly ichthyoplankton cruises from December 1981 to April 1982. Ranked in order of abundance these species were sand seatrout, *Cynoscion arenarius*; Atlantic croaker, *Micropogonias undulatus*; spot, *Leiostomus xanthurus*; black drum, *Pogonias cromis*; southern kingfish, *Menticirrhus americanus*; and banded drum, *Larimus fasciatus*. Total larva density was highest in April, and the high densities were associated with the coastal boundary layer, a horizontal density front caused by an intrusion of fresher water onto the inner shelf that probably issued from the Atchafalaya River east of the study area. Spawning by sand seatrout began in January, two months earlier than previously reported, and first occurred offshore of midshelf but moved shoreward as the season progressed. Analysis of length-frequency data suggest that spot probably began to spawn in November, one month earlier than once thought. Both sand seatrout and Atlantic croaker larvae were captured at higher rates at night than during the daytime. Sand seatrout larvae appear to be somewhat surface oriented while spot may undergo vertical migration. Interpretation of the sciaenid data support a previously developed transport hypothesis involving gulf menhaden larvae and west-northwest alongshore advection within and just outside of a horizontally stratified coastal boundary layer.

Members of the perciform family Sciaenidae are an important sport and commercial fishery resource along the United States coast of the Gulf of Mexico and are perhaps the most prominent group of northern Gulf inshore fishes. Sciaenids exceed all other families in numbers of species (18) and in numbers of individuals or biomass; they are among the top four families with Mugilidae, Engraulidae, and Clupeidae (Gunter 1938, 1945; Moore et al. 1970; Franks et al. 1972; Hoese and Moore 1977). Of the six species of sciaenids captured during this study, only the banded drum, *Larimus fasciatus*, is not commonly sought by both sport and commercial fishermen.

Many of Louisiana's sciaenids spawn in coastal or offshore waters. They have pelagic eggs and young which are then transported into estuaries (Johnson 1978 for review). The seasonal importance of Louisiana's estuaries as nursery grounds for postlarval and juvenile sciaenids is well documented (Cowan 1985 for review), and several summary works are available which contain taxonomic and biological information on adult sciaenids (Pearson 1929; Suttkus 1955; Guest and Gunter 1958; Hoese and Moore 1977; Johnson 1978; Powles and Stender 1978; Barger and Johnson 1980; Barger and Williams 1980; Mercer 1984a, b). In contrast, there is little information about sciaenid ichthyoplankton assemblages in Gulf continental shelf waters, their offshore and coastal distribution, or the oceanic current systems which influence their estuarine recruitment.

This study provides such early life history information by determining larva distribution, abundance, and length frequency; by documenting spawning location (depth and distance from shore) of winter and early spring-spawned sciaenids off west Louisiana; and by analyzing larval sciaenid distribution with respect to known water circulation patterns and a larval gulf menhaden, *Brevoortia patronus*, transport hypothesis in the shelf waters of the northwestern Gulf of Mexico (Shaw et al. 1985b). Recruitment implications of the observed distribution, larva age structure, and transport of sciaenids in Louisiana waters are also discussed.

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METHODS AND MATERIALS

Detailed sampling methodology has been presented elsewhere (Shaw et al. 1985 a, b). Briefly, larval sciaenids were collected off west Louisiana on a sampling grid consisting of 37 stations on 5 transects (Fig. 1) during 5 midmonthly cruises from December 1981 to April 1982. Ichthyoplankton samples were analyzed from the 335 μm mesh net side of an opening and closing, 60 cm, paired "bongo type" plankton sampler fitted with General Oceanics[4] flowmeters (model no. 2030). Most plankton collections (125 of 187 total) consisted of 10-min stepped oblique tows from near bottom to surface. Nets were set closed and opened just prior to the stepped ascent. Each tow had five steps with a retrieval rate between steps of 20 m/minute; towing speed was about 1 m/second (2 knots). The object of the 10-min tow was to filter approximately 100 m^3 of water. This process increased the water volume filtered per unit depth at the shallow stations relative to deeper stations. This discrepancy is acceptable since the alternative would be to compare 17-s shallow-station oblique tows with 9-min deep-station tows at a uniform retrieval rate (Houde 1977). At selected stations (A-3, 6, 9; B-1; C-6; D-1; E-3, 6, 9; Fig. 1), only 10-min simultaneous surface and near-bottom horizontal tows (31 surface and 31 near-bottom) were made to determine if sciaenid larvae were vertically stratified. Larva total length (TL) was measured to the nearest 0.1 mm. Larva densities are reported as standardized catch rates at a station (density = larvae/100 m^3).

A four-way analysis of variance (ANOVA) was performed on $\log_{10}$ transformed [(no. larvae/100 m^3) + 1] data to determine the spatial (vertical and horizontal), temporal, and diel patterns of species density and distribution. The four main effects tested were month (January–April); station depth group (d.g.) (d.g. 1 ≤ 10 m, 10 m < d.g. 2 ≤ 14 m, 14 m < d.g. 3 < 24 m and d.g. 4 ≥ 24 m); day-night (2000 hours ≤ night ≤ 0500 hours); and horizontal tow type (surface vs. near-bottom). Data from the December cruise were not included as only the A transect was completed due to adverse weather conditions.

Two methods of current estimates were utilized (following Shaw et al. 1985b): 1) instantaneous current profiles taken at each station and 2) continuous surface and near-bottom current meter measurements at two sites (H and S; Fig. 1). The instantaneous number of larvae transported on each transect was calculated by using the equation $D \times \overline{U} \times M$ = number of larvae per meter per second where D = larva density (larvae/m^3) from either oblique tows or from the mean of the horizontal tows (i.e., average of surface and near-bottom catch rates), $\overline{U}$ = depth-averaged water velocity (m/s) determined from instantaneous current meter profiles at each station, and M = water depth (m) at each station.

Distribution diagrams and length-frequency histograms were generated for each cruise for the three most abundant sciaenid species. Inspection of these data along with current measurements allowed a comparison with the previously mentioned transport hypothesis.

RESULTS AND DISCUSSION

Total Sciaenids

A total of 5,225 larval sciaenids accounted for 9.1% of the fish larvae collected. In December through February, samples were dominated by Atlantic croaker, *Micropogonias undulatus*, and spot, *Leiostomus xanthurus*. In March and April samples contained mostly sand seatrout, *Cynoscion arenarius*. In all, six species of sciaenid larvae were collected: sand seatrout (N = 4,100); Atlantic croaker (N = 567); spot (N = 264); black drum, *Pogonias cromis* (N = 68); southern kingfish, *Menticirrhus americanus* (N = 53); and banded drum (N = 13). Additional *Menticirrhus*, not identifiable to species, accounted for 160 more specimens (Table 1). A more detailed examination of the data on the three most abundant sciaenid species follows.

Sand seatrout, *Cynoscion arenarius*

A total of 4,100 sand seatrout larvae was collected making it the most abundant sciaenid taken during the study. Larval sand seatrout densities were highest in April (Table 1) with a mean of 46.1 larvae/100 m^3; mean density in February and March was 0.3 and 2.9/100 m^3, respectively, and 1 larva was collected in January. Larvae were distributed mostly over the midshelf in February but highest concentrations were later found inshore and towards the east (Fig. 1). Over the course of study, larvae were found in temperatures and salinities ranging from 14° to 21°C and

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

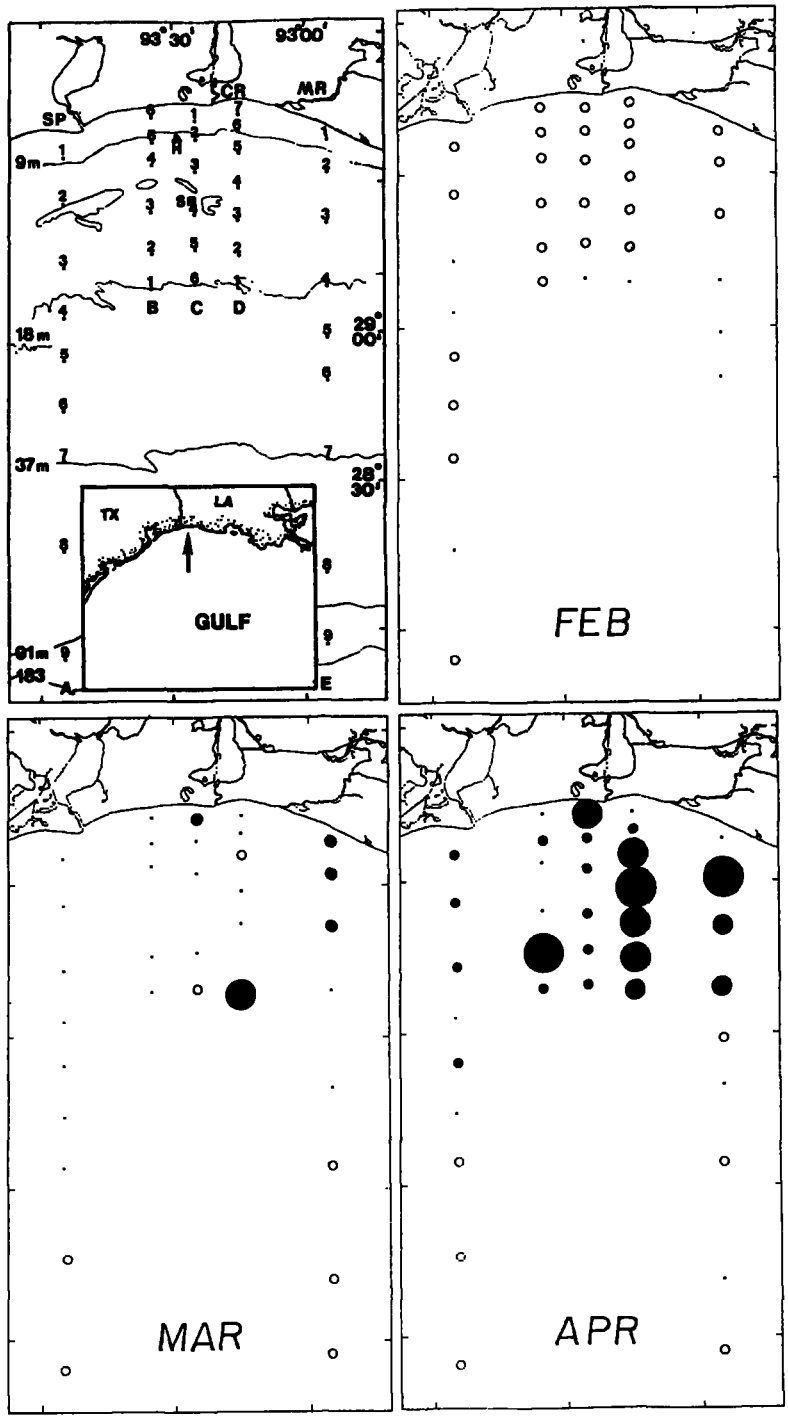

FIGURE 1.—Density distribution of sand seatrout, *Cynoscion arenarius*, larvae by month, February–April 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types. Also shown is the station sampling grid with moored current meter sites (H and S) and selected isobaths. SP = Sabine Pass, CR = Calcasieu River, and MR = Mermentau River.

TABLE 1.—Total number, months of occurrence and monthly density of sciaenid larvae collected in west Louisiana shelf waters from December 1981 to April 1982.

Taxa	Total number	Months of occurrence and density (No./100 m³)				
		Dec.	Jan.	Feb.	Mar.	Apr.
Cynoscion arenarius	4,100	—	1 larva	0.3	2.9	46.1
Micropogonias undulatus	567	2.0	2.2	3.2	2.2	0.2
Leiostomus xanthurus	264	7.8	1.3	0.9	0.1	—
Menticirrhus sp.	160	—	—	—	—	1.9
Pogonias cromis	68	—	1 larva	0.5	0.2	0.2
Menticirrhus americanus	53	—	—	—	—	0.6
Larimus fasciatus	13	—	—	—	—	0.2

from 15 to 36 ppt (Table 2) and at station depths ranging from 5 to 70 m, but most were collected inside the 18 m isobath. Larval sand seatrout density increased in April with many stations exhibiting densities in excess of 250 larvae/100 m³; the larvae appeared to be associated with a freshet of water on the shelf, probably issuing from the Atchafalaya River east of the study area (Shaw et al. 1985a). The presence of riverine runoff on the shelf, which was most evident in March and April 1982, caused the development of an oceanic salinity front referred to as the coastal boundary layer, 10–35 km from shore (Wiseman et al. 1987).

Observed spawning seasonality and location for sand seatrout are in part consistent with previously published information (Shlossman and Chittenden 1981 for review). The presence of a 4 mm TL larva in January indicates some spawning had taken place at least 2 months earlier than

TABLE 2.—Monthly data summaries at time of capture for three sciaenid larvae (*Cynoscion arenarius*, *Micropogonias undulatus*, and *Leiostomus xanthurus*) collected in west Louisiana shelf waters from December 1981 to April 1982.

Species/month	Total number	Length range (mm TL)	Temperature range (°C)	Salinity range (ppt)	Depth range (m)
Cynoscion arenarius					
January	1	4	14	35	18
February	20	2.5–4.5 (mode = 2–3)	14–20	34–36	15–70
March	203	1.5–10.5 (mode = 2–3)	14–18	25–36	5–40
April	3,876	1.5–20.5 (mode = 2–3)	20–21	15–36	5–70
Micropogonias undulatus					
December	28	2.5–10.5 (mode = 3–4)	12–20	30–36	10–65
January	158	2.5–10.5 (mode = 4–5)	10–18	30–36	5–70
February	221	2.5–17.5 (mode = 14–15)	11–17	27–36	5–40
March	144	2.5–19.5 (mode = 14–15)	14–20	25–36	5–115
April	16	11.5–18.5 (mode = 17–18)	20.5	22	7
Leiostomus xanthurus					
December	110	2.5–7.5 (mode = 3–4)	14–18	30–36	16–65
January	89	2.5–13.5 (mode = 4–5)	10–18	30–36	5–40
February	62	3.5–15.5 (mode = 12–13)	10–17	28–36	5–40
March	3	3.5–16.5	14–17.5	26–36	11–40

previously reported. Monthly length-frequency data for sand seatrout show that larvae as large as 11 mm TL were first present in March samples (Fig. 2A). Based on the estimated growth rate determined for sand seatrout (Cowan 1985; Shaw et al., in press), an 11 mm larva could be as old as 65 days; this further supports January spawning. Sand seatrout are reported to spawn from March to August, during two discrete periods—one in March–May, the other August–September, with little spawning between the two peak periods (Hoese 1965; Daniels 1977; Shlossman and Chittenden 1981).

An examination of distribution and length-frequency data (Figs. 1, 2A) suggests that most spawning initially took place in midshelf to offshore waters at depths ranging from 15 to 80 m or to about 175 km from shore. As the season progressed into March and April, spawning location, as determined by the presence of larvae <3.0 mm TL, was more inshore (5–18 m) with few small larvae occurring at depths >25 m.

Other than the indication that spawning may move from offshore to inshore waters as the season progresses, this spatial information agrees with the limited life history data available on sand seatrout. Most spawning has been shown to occur in the shallow waters of the Gulf of Mexico, primarily between 7 and 15 m in depth (Gunter 1945; Moffet et al. 1979; Shlossman and Chittenden 1981). Running ripe *C. arenarius* have been captured in deepter waters (70–90 m) in February and March, but no spawning was indicated (Franks et al. 1972; Perry 1979).

In a four-way ANOVA employed to determine patterns of larval sand seatrout density and distribution, month was a highly significant main effect ($P < 0.01$; Table 3) reflecting spawning seasonality and the magnitude of the density increase in April. The test for interaction between month and day-night was employed to determine if daytime gear avoidance was evident as size and mobility of larva increased. Most sand seatrout collected, however, were small and no clear monthly modal increase in larva size was evident (Fig. 2A). The significant interaction ($P < 0.01$) was probably due to an increased catch in oblique tows at night as the season progressed (0.0 in January, 64.9/100 m^3 in April). The significant interaction between month and depth group and the highly significant depth group main effect ($P < 0.01$) represents the shift in larva concentration from midshelf early in the study, to a more coastal distribution in March and April (Fig. 1). Mean larva density was greatest in depth group 1 (23.7/100 m^3) followed by depth groups 2, 3, and 4 (12.7, 9.2, and 0.3/100 m^3, respectively). The third main effect, day vs. night tows, was highly significant ($P < 0.01$); many more sand seatrout larvae were collected at night (averge catch rates in all night (74) tows combined = 21.6/100 m^3 vs. day (113) tows = 7.4/100 m^3). Highest nighttime catches occurred in oblique (49) tows (26.9/100 m^3) while the day-oblique-catch rate averaged 7.6/100 m^3 in 76 tows. Overall, average catch rate was highest in oblique (125) tows (14.6 larvae/100 m^3), followed by surface (31) tows (9.2/100 m^3), and then bottom (1.9/100 m^3; 31 tows). Intrepretation of the data suggests that

TABLE 3.—Summary data from four-way analysis of variance done on $\log_{10}$ transformed [(larvae/100 m^3) + 1] data from ichthyoplankton samples collected from January to April 1982. The results are for A. *Cynoscion arenarius*, B. *Micropogonias undulatus*, and C. *Leiostomus xanthurus*. The four main effects tested were months (Jan.–Apr.), station depth group (d.g. 1 ≤ 10 m, 10 m < d.g. 2 ≤ 14 m, 14 m < d.g. 3 < 24 m and d.g. ≥ 24 m), day - night (2000 hours ≤ night ≤ 0500 hours) and horizontal tow type (surface vs. near-bottom).

Source	df	PR > F	
A. Dependent variable: $\log_{10}$ [(*Cynoscion arenarius*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.75$
Month	3	0.0001**	
Depth group	3	0.0001**	
Day-night	1	0.0026**	
Horizontal tow type	1	0.2574 (NS)	
Month vs. Day-night	3	0.0001**	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.4180 (NS)	
Error	177		
Corrected Total	198		
B. Dependent variable: $\log_{10}$ [(*Micropogonias undulatus*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.63$
Month	3	0.0045**	
Depth group	3	0.3551 (NS)	
Day-night	1	0.0001**	
Horizontal tow type	1	0.4448 (NS)	
Month vs. Day-night	3	0.2168 (NS)	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.1288 (NS)	
Error	177		
Corrected Total	198		
C. Dependent variable: $\log_{10}$ [(*Leiostomus xanthurus*/100 m^3) + 1]			
Model	21	0.0001**	$r^2 = 0.51$
Month	3	0.0001**	
Depth group	3	0.0033**	
Day-night	1	0.1875 (NS)	
Horizontal tow type	1	0.3216 (NS)	
Month vs. Day-night	3	0.2138 (NS)	
Month vs. Depth group	9	0.0001**	
Day-night vs. Tow type	1	0.0324*	
Error	177		
Corrected Total	198		

* = Statistically significant ($P < 0.05$).
** = Highly significant ($P < 0.01$).
(NS) = Not significant.

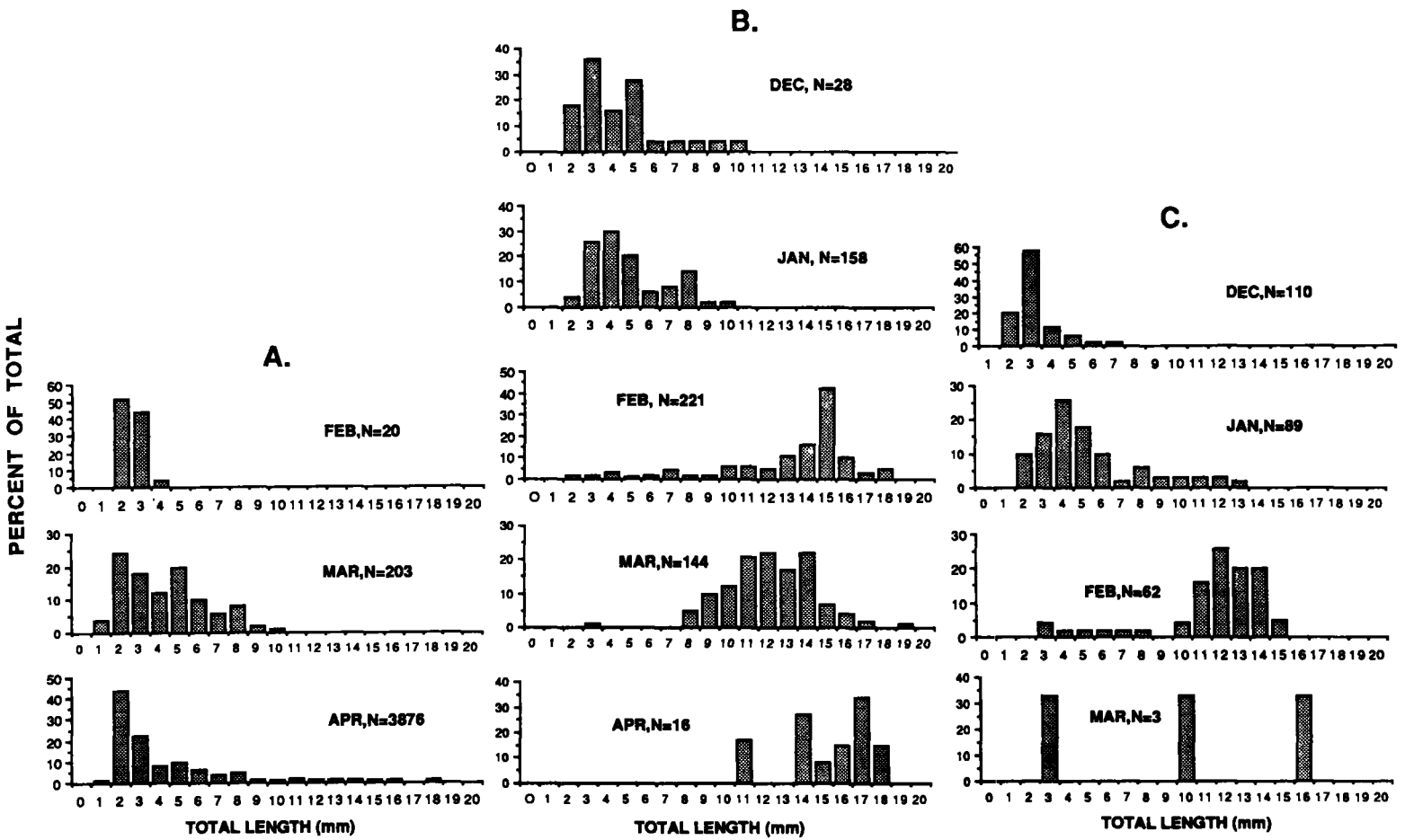

FIGURE 2.—Length-frequency data by month for larval sciaenids, December–April 1982. A. *Cynoscion arenarius*, B. *Micropogonias undulatus*, and C. *Leiostomus xanthurus*. N = total number caught and measured.

sand seatrout larvae were somewhat surface oriented.

Atlantic croaker, *Micropogonias undulatus*

The second most abundant sciaenid taken was Atlantic croaker ($N = 567$). Larval Atlantic croaker density was greatest in February at 3.2/100 m^3, but density was relatively constant from December through March (Table 1). Mean densities for December, January, March, and April were 2.0, 2.2, 2.2, and 0.2/100 m^3, respectively. Atlantic croaker was the only sciaenid collected in all months of the study. Their overall distribution (all sizes combined) was generally uniform over most of the shelf (Fig. 3) except in March and April when they were more often found inshore. Recently spawned larvae (<3.0 mm TL) were also collected over much of the shelf at station depths ranging from 15 to 115 m or from about 20 to 200 km from shore. However, most small larvae were collected near midshelf about 65–125 km from shore. In December and January the majority of the larvae were small. By April, no recently spawned individuals were collected (Fig. 2B). For the study overall, larvae were found in salinities and temperatures ranging from 22 to 36 ppt and from 10° to 20.5°C (Table 2).

Spawning by Atlantic croaker in Gulf of Mexico waters is reported to occur from September to March, with a distinct peak in October (Hoese 1965; Sabins and Truesdale 1974; White and Chittenden 1977; Benson 1982) and to occur primarily offshore over a wide area (Pearson 1929; Hildebrand and Cable 1930; Wallace 1940; Haven 1957; Bearden 1964; Hoese 1965; Nelson 1967). Atlantic croaker larvae, however, have been taken on the outer continental shelf off Texas from September to May (Finucane et al. 1979).

As with sand seatrout, a four-way ANOVA was used to determine patterns in larva density and distribution (Table 3). Larval Atlantic croaker density by month was a highly significant main effect ($P < 0.01$). Densities at the end of their spawning period were low, increased only slightly in February, and then dropped off by April (Table 1). The interaction between month and day-night was not significant. The highly significant interaction between month and depth group was not surprising. Larvae were in more offshore waters early in the study while later becoming more abundant inshore (Fig. 3). However, as a main effect, depth group was not significant. Larval Atlantic croaker mean densities for depth groups 1 through 4 were 3.9, 0.8, 0.4, and 0.7/100 m^3, respectively. Day-night, as a main effect, was highly significant ($P < 0.01$). Larval Atlantic croaker density was over 5 times higher at night (all tow types combined) than during the day (3.7 vs. 0.7/100 m^3). However, the interaction between day-night and horizontal tow type was not significant. The fourth main effect tested, horizontal tow type, was not significant. Average catch rates at the surface and near-bottom were similar (1.0 and 1.8/100 m^3, respectively).

Spot, *Leiostomus xanthurus*

The third most abundant sciaenid collected was spot ($N = 264$). Density of spot larvae was highest in December at 7.8 larvae/100 m^3 (Table 1). However, the high December value must be viewed with a consideration of the abbreviated cruise track for that month and the resultant reduction in spatial coverage. Mean densities for January to March were 1.3, 0.9, and 0.1/100 m^3, respectively. No spot larvae were collected in April. In general, larva density was low and their distribution was uniform over the shelf out to the 40 m isobath, about 130 km offshore (Fig. 4). Spot were collected in temperatures and salinities ranging from 10° to 18°C and from 26 to 36 ppt (Table 2), and at stations with depths ranging from 5 to 65 m.

Larvae >7 mm TL in our mid-December (Fig. 2C) collections and small larvae (<3.0 mm TL) in all but the last cruise indicate that spawning probably began by at least November and continued through March. Spawning occurred from near midshelf (about 65 km) out to 175 km from the coast. Data presented here partly concur with previously published information on spot spawning periodicity. In the northern Gulf, spawning reportedly occurs from late December to March, peaking in January, and takes place well offshore in moderately deep water (Pearson 1929; Kilby 1955; Townsend 1956; Dawson 1958; Springer and Woodburn 1960; Pacheco 1962; Nelson 1967; Joseph 1972; Music 1974; Sabins and Truesdale 1974).

A four-way ANOVA indicated that month, as a main effect for spot larvae, was highly significant ($P < 0.01$), which probably reflects the decreasing catch rates seen from January to March (Table 3). The interaction between month and depth group was also highly significant ($P < 0.01$) as was depth group as a main effect. Larval spot

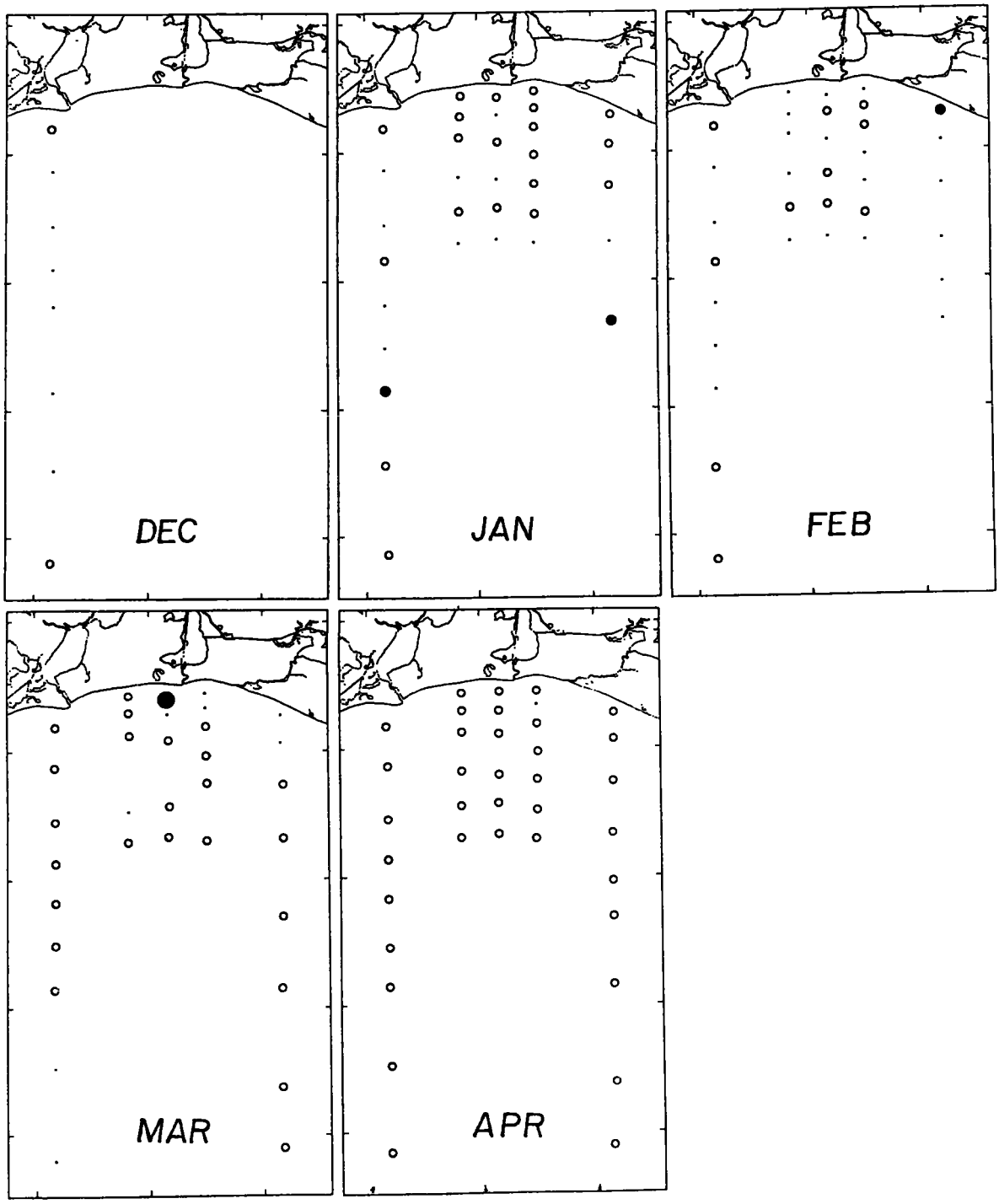

FIGURE 3.—Density distribution of Atlantic croaker, *Micropogonias undulatus*, larvae by month, December 1981—April 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50;–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types.

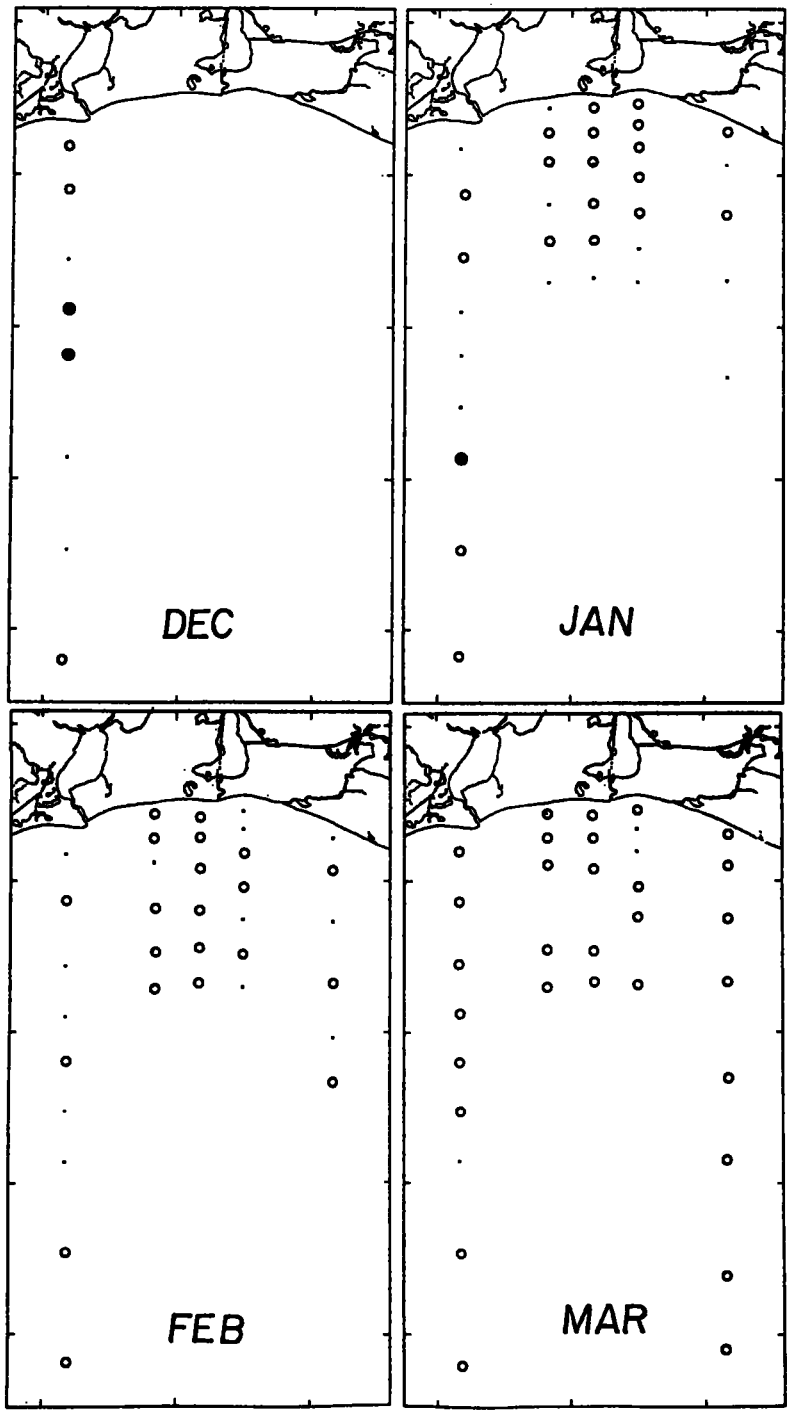

FIGURE 4.—Density distribution of spot, *Leiostomus xanthurus*, larvae by month, December 1981–March 1982. Densities are as follows: o = 0; · >0–10; • >10–50; ● >50–99; ● >99–250; ● >250/100 m^3 of water filtered from all plankton tow types.

densities were higher offshore in the early part of the study and then greater inshore during February and March. Depth group 4 had the highest mean density (1.3/100 m^3) followed by depth groups 1 and 3 (0.4/100 m^3 each) and depth group 2 (0.1/100 m^3). Day-night comparisons proved nonsignificant as a main effect for spot larvae. The average catch rates for all day and night tows were identical (0.5/100 m^3). However, the interaction between day-night and horizontal tow type was statistically significant ($P < 0.05$). In this case, vertical migration and stratification may be indicated. Average catch rate of spot larvae during the day at the surface was 0.1/100 m^3, while near the bottom it averaged 1.6. Conversely, nighttime average catch rate at the surface was 1.0/100 m^3, while the near-bottom rate averaged 0.04. These are very low densities but the vertical differences are an order of magnitude and their reversing pattern suggests that spot larvae were stratified and undergoing diel vertical migration. Daytime bottom and nighttime surface average catch rates were higher than for oblique (O) tows (day, O = 0.45/100 m^3; night, O = 0.49/100 m^3). Average catch rates for surface and near-bottom tows, regardless of time of day, were 0.5 and 0.9/100 m^3, respectively.

As previously mentioned, other larval sciaenid species (i.e., black drum, banded drum, southern kingfish) were collected during these cruises. However, relatively few individuals were captured (Table 1), making information on their distribution inconclusive.

TRANSPORT ANALYSIS

Alongshore advection within and just outside the coastal boundary layer in the northwestern Gulf of Mexico has been hypothesized as the major mechanism transporting gulf menhaden larvae to the estuaries in western Louisiana, rather than across-shelf transport from directly offshore. In contrast, such direct across-shelf transport has been demonstrated for sciaenids and other species along the U.S. mid-Atlantic coast (Nelson et al. 1976; Norcross and Austin 1981; Miller et al. 1984). The data collected for sciaenid larvae (all species combined) were examined in light of this Gulf hypothesis. Larval sciaenid densities were less than those for gulf menhaden but similarities in distribution were evident. Both larval sciaenid and gulf menhaden densities were highest at midshelf early in the study. By March and April the highest densities were found towards the east and inshore and were associated with a horizontal density front (coastal boundary layer) caused by an intrusion of fresher water onto the shelf.

The along-transect length-frequency patterns exhibited by larval sciaenids and gulf menhaden were also similar. No apparent increase in size was seen until gulf menhaden larvae were on the inner shelf or sciaenids were on the mid- to inner shelf. The expected pattern of a gradual increase in larva size from offshore to inshore, which would result if there were significant across-shelf (south to north) transport, was not evident in either data set. Off the North Carolina coast, Warlen (1981) and Miller et at. (1984) showed that ages and lengths of both spot and Atlantic croaker larvae increased systematically toward shore in an area where winter water currents favored across-shelf (west to east) transport.

During the winter of 1981–82, moored current meter data from sites H and S (Fig. 1) indicated that flow was directed primarily alongshore in the west-northwest direction. Several researchers have reviewed the circulation in the northwestern Gulf (Nowlin 1971; Kelly et al. 1982; Crout 1983). It was not until Cochrane and Kelly (1986) developed their comprehensive circulation model for the Louisiana-Texas continental shelf, however, that the ocean current patterns, which led to the hypothesized larva transport model, were fully documented. Flow in nearshore coastal waters is westward all year except in summer when it usually reverses, while farther offshore flow is eastward all year (Cochrane and Kelly 1986).

To quantify transport, larval sciaenid densities were combined with the vertically averaged, instantaneous current measurements. The resultant curves present the number of larvae transported per unit time at each station (Fig. 5). Early in the winter, highest sciaenid larva transport (mostly Atlantic croaker and spot) was located midshelf. Later (March and April), transport values were higher inshore and reflected the increase in larval sciaenid density (primarily sand seatrout). Overall, larva transport was primarily westward and ranged from about 0.05 to 4.0 larvae/meter per second.

Although the oceanographic data collected were insufficient to precisely quantify onshore transport rates, an estimate was obtained by using the mean current vectors from the near surface meter at site H (Fig. 1) from 24 January to 12 May 1982 (14.33 cm/second alongshore westward

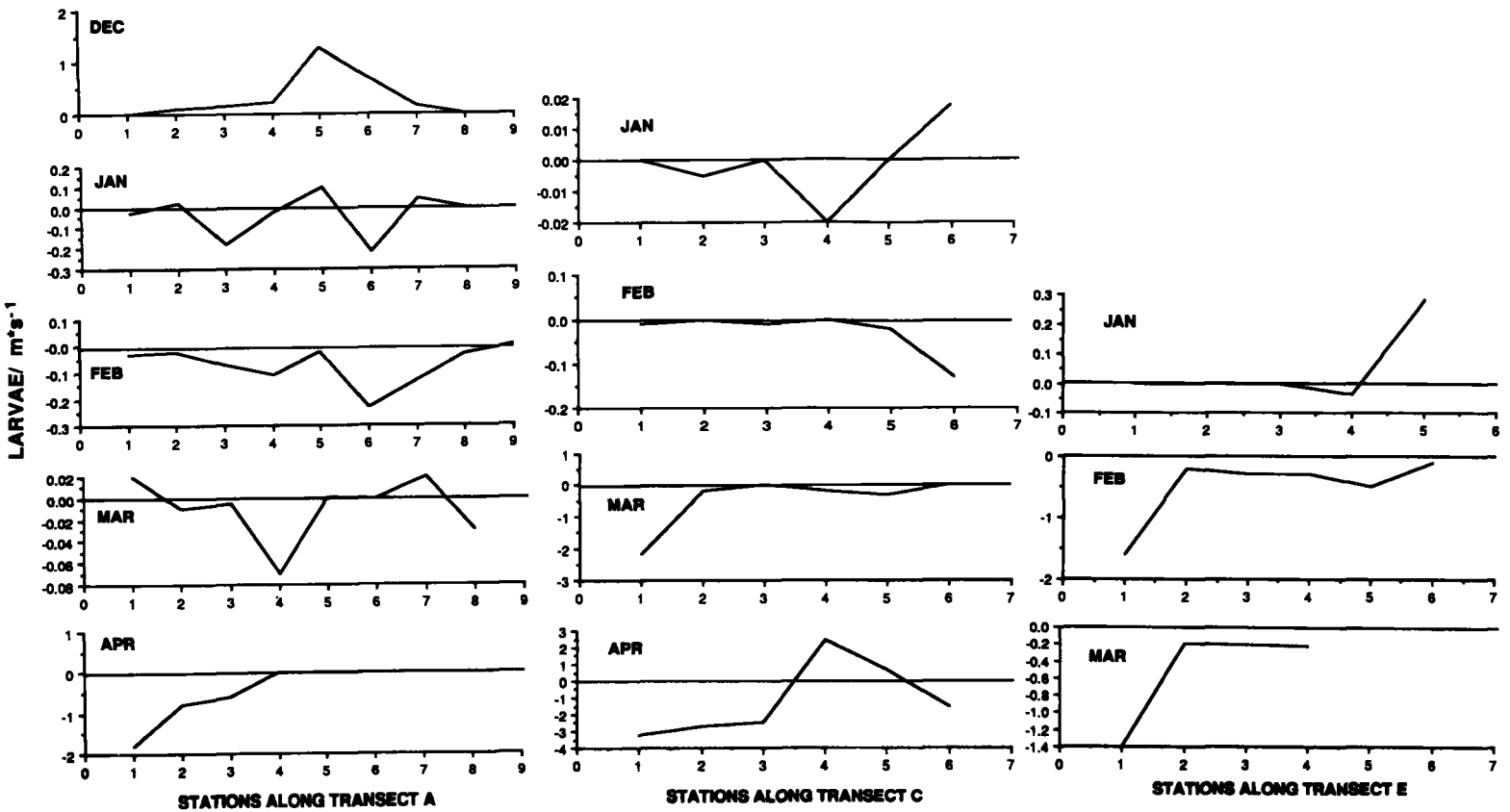

FIGURE 5.—Larval sciaenid transports (larvae/m·s) across transect A, C, and E, December 1981–April 1982. Easterly transports are positive values. Transport rates were determined from the observed larva concentrations combined with instantaneous current measurements. Note the difference in scale between months.

and 1.75 cm/second shoreward). Based on that average shoreward advection rate we calculated that larvae could be passively transported 98 km in the onshore direction in 65 days. Examination of length frequency and age at capture data (Cowan, in press) suggest that larval Atlantic croaker arrive in nearshore coastal waters, on the average, 60–90 days after hatching. Most small, newly hatched Atlantic croaker larvae were collected approximately 100 km offshore. Although the onshore component of advective transport is small in comparison with the average alongshore component, the estimate of shoreward transport rate is reasonable when age of larvae is considered.

CONCLUSIONS— RECRUITMENT IMPLICATIONS

Across-shelf transport appears to be an order of magnitude smaller than alongshore advective transport in the northwestern Gulf shelf waters during winter and spring. Sciaenid larvae collected offshore in the study area, at midshelf and beyond, would probably be lost to the estuaries in western Louisiana. Those offshore larvae would be transported towards north Texas estuaries, or back to the east if they were far enough offshore, since there is evidence for an easterly counter current (Kelly et al. 1982; Cochrane and Kelly 1986).

Sand seatrout are common in west Louisiana estuaries (Herke et al. 1984) and were the most abundant sciaenid larvae collected in this study. They spawn, in general, more inshore (Fig. 1) than Atlantic croaker or spot. Conceivably, many of the sand seatrout collected in the study area inside the coastal boundary layer on the inner shelf would have recruited to Louisiana estuaries.

Still, large numbers of postlarval sciaenids, other than sand seatrout, enter the estuaries in west Louisiana each year. Atlantic croaker and spot were the 3rd and 21st most abundant fish, of 117 species collected, in the Calcasieu River Basin, the largest estuary in west Louisiana (Herke et al. 1984). However, the distribution and transport analyses indicate that most spot and Atlantic croaker larvae directly offshore at least would not have recruited to the Calcasieu Basin. Interpretation of these data suggests that the source of the sciaenid postlarvae shown to seasonally recruit to the Calcasieu estuaries must be east of the study area. Interpretation of data summarizing several years of northern Gulf shrimp-trawl collections suggests that, during the spawning season, a sufficient concentration of adults exists to the east of our study area (Darnell et al. 1983).

In the fall and winter, high concentrations of Atlantic croaker, and to a lesser extent spot, have been found between the 20 and 40 m depth contours (65 and 125 km offshore) in an area east of the sampling grid. The area and timing of high concentration coincides with the reported spawning location and period for both Atlantic croaker and spot. If indeed this concentration represents a spawning distribution, it would help explain why so few Atlantic croaker and spot larvae, relative to the number of juveniles seen in estuaries, were collected in this and previous Gulf of Mexico ichthyoplankton studies. Unless collections were made in or near the spawning area, single-station densities would be low as eggs and larvae were dispersed. Furthermore, this study demonstrates the need for understanding both biological (vertical distribution, age and growth, behavior, etc. of larvae) and physical (ocean currents, estuarine-shelf exchange, etc.) processes which may influence estuarine recruitment.

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BEHAVIOR OF SOUTHERN RIGHT WHALES, *EUBALAENA AUSTRALIS*, FEEDING ON THE ANTARCTIC KRILL, *EUPHAUSIA SUPERBA*

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ABSTRACT

Southern right whales, *Eubalaena australis*, were observed in 3 successive years on the western side of the Antarctic Peninsula. These whales do not appear to be from the well-documented Valdes, Argentina population. The whales we observed were feeding on Antarctic krill, *Euphausia superba*. When krill were at the surface right whales surface-skimmed at high speed, with upper jaw lifted above the water surface. In heavy weather one right whale "tail-sailed" at slow speed, with head submerged and apparently feeding. When krill were organized in subsurface schools, right whales engaged in subsurface feeding, diving repeatedly in place, apparently working a given school. One whale swam directionally to the only known large school of krill in the area and fed intensively, rested on the surface, then began a second feeding bout. Whales hyperventilated, false fluked, and fluked prior to feeding dives. These are the first detailed observations of feeding behavior of right whales in Antarctic waters and suggest that coastal Antarctica may have been (and may become again) a regular part of the summer feeding range of the species.

Right whales are among the rarest of the great whales, having been hunted almost to extinction a century ago. The southern right whale, *Eubalaena australis*, has been studied only recently and only during the austral winter when the whales aggregate inshore to bear calves and to mate (Clarke 1965; Payne 1976, 1986; Best 1981; Aguayo and Torres 1986). Because right whales were commercially extinct by the mid-1850's, very little has been learned about their ecology from the 20th century whaling industry. Information on feeding, migration, stock structure, and reproductive biology was collected for most other Antarctic mysticete whales during the heyday of whaling in this century (e.g., Mackintosh 1965; International Whaling Commission reports 1964-present). The small number of surviving right whales (ca. 2% of historic levels in the Southern Hemisphere, Breiwick and Braham 1984) has made it difficult for researchers to study this species. Our current understanding of its feeding and calving ecology in the Southern Hemisphere comes from observations made primarily off Peninsula Valdes, Argentina (Payne 1986).

In Antarctic waters south of lat. 60°S, more than 30 sightings of right whales have been reported previously (Berzin and Vladimirov 1981; Goodall and Galeazzi 1986; Ohsumi and Kasamatsu 1986). Most were in the vicinity of the South Orkney Islands, 9 were near the Antarctic Peninsula, 6 were in the Pacific sector of the Antarctic, and 2 were south of Africa. We have observed southern right whales during 3 consecutive austral summers near the western shore of the Antarctic Peninsula, and the sightings reported herein and in Stone and Hamner (in press) are the most southerly as well as the most detailed observations.

We sighted one individual during the 1983–84 austral summer (also recorded by Captain P. Lenie in the log of the RV *Hero*; Goodall and Galeazzi 1986), two individuals in 1984–85, and eight in 1985–86, four of which we individually identified. In 1986 a fortunate combination of fair weather and available ship time permitted us to make the first extended uninterrupted observations on the behavior of right whales feeding on the Antarctic krill, *Euphausia superba*.

METHODS

Right whales are distinguished by the absence of a dorsal fin and regions of cornified skin (callosities) on the head, jaws, and chin. Individual whales were identified by standard methods, using video tapes and telephotographs of head callosities and scarring patterns on the head and back (Payne et al. 1983; Kraus et al. 1986). When possible, we dropped large disks of plywood of

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known diameter next to the whale and included it in the photograph to measure whale size.

Behavioral patterns were observed from the ship's bridge and recorded on a portable computer as they occurred, using a program which timed entries of encoded behaviors or coments to the nearest second. Krill schools were recorded on a Simrad echosounder and the identity of the organisms causing the echograms was verified by net samples taken with an Isaacs-Kidd midwater trawl and by divers' visual confirmation of krill schools near the surface.

RESULTS

7 January 1984: At 0500 hour, north of Cape Murray near Two Hummock Island, one right whale was feeding at the surface with its upper jaw lifted above the water, swimming at high speed (estimated at 8–9 knots by the ship's captain) in feeding runs of 15–20 seconds, which we recorded on video. Three humpback whales nearby were diving in one specific location. The right whale repeatedly changed direction between surface runs so that its horizontal directional feeding excursions did not take it far from the vicinity of the vertically diving humpbacks. During these powerful filter-feeding runs enormous amounts of water were displaced, cascading beside and behind the right whale and producing a large wake.

15 January 1985: A cow and a calf were swimming slowly at the surface some 500 m from the eastern shore of Anvers Island. On approach by the ship the whales swam slowly into shallow water where we could not follow. It was near dusk and we could not get photographs for future identification.

7 January 1986: We encountered one southern right whale and six humpbacks at 1830 hour at lat. 63°46'S, long. 61°13'W, between Trinity and Hoseason Islands. We photographed the head and body of the right whale for subsequent identification. We followed the whale for approximately 2 hours, recording diving times, surface intervals, and breathing rates. The whale frequently changed directions underwater and consequently we often failed to see the whale immediately when it resurfaced, so breathing rate data for this behavioral sequence are incomplete. The whale appeared to have captured krill on at least one dive because when the whale surfaced it repeatedly and briefly opened and closed its mouth, with baleen visible, a behavior presumably associated with separation of krill and water prior to swallowing the prey (Watkins and Shevill 1976). About 50 cape petrels, *Daption capensis*, alighted on the water and fed at the surface around the whale. When the whale's jaw movements ceased, the birds soon stopped feeding, but they remained on the water and did not follow the whale when it swam away at the surface.

2 March 1986: We observed one right whale at the northern end of the Neumayer Channel, where a large iceberg was grounded on a 93-fathom rise 2 miles east of Iceberg Point. The wind was blowing from the north at 20-24 knots and a strong surface current was flowing south, producing a bow wave on the grounded iceberg. The right whale repeatedly swam NE of the berg, raised its tail high out of the water at 90° to the wind, submerged its head, and "sailed" downwind past the iceberg, a behavior previously noted for right whales in Argentina (Payne 1976). Soon after we first saw the whale, it stopped tail-sailing and began diving, still along the N-S transect near the iceberg where it had been sailing. The presence of the ship did not cause the whale to alter its back-and-forth swimming rhythm or direction. We waited until the whale began one of its N-S transects past the iceberg and followed about 100 m behind it with the ship. A large school of krill was present on the east side of the iceberg. We recorded no other schools in the vicinity. The whale was accompanied by three female fur seals. The seals constantly darted about the head of the whale when it surfaced after long dives and appeared to annoy the whale, because several times the whale repeatedly slashed its head sideways when the seals swam too close.

3 March 1986: At 1030 hour, we spotted a single southern right whale near the mouth of Andvord Bay on the Antarctic Peninsula. The whale was swimming SSW at about 3 knots, making short dives that lasted about 19 seconds ($N = 12$, SD = 9.0 seconds), with brief surface intervals that averaged 6.1 seconds ($N = 12$, SD = 2.6 seconds) (Fig. 1). The whale then stopped diving but continued to swim SSW toward the NE tip of Lemaire Island, swimming mostly at the surface for approximately 90 minutes. During this period the whale appeared unconcerned with the ship, which remained 50–100 m behind it, but when the whale neared an iceberg that was hard aground near Lemaire Island, it turned suddenly at a right angle to its prior course and swam between the iceberg and the rocks. The ship was nonetheless able to follow the whale through the

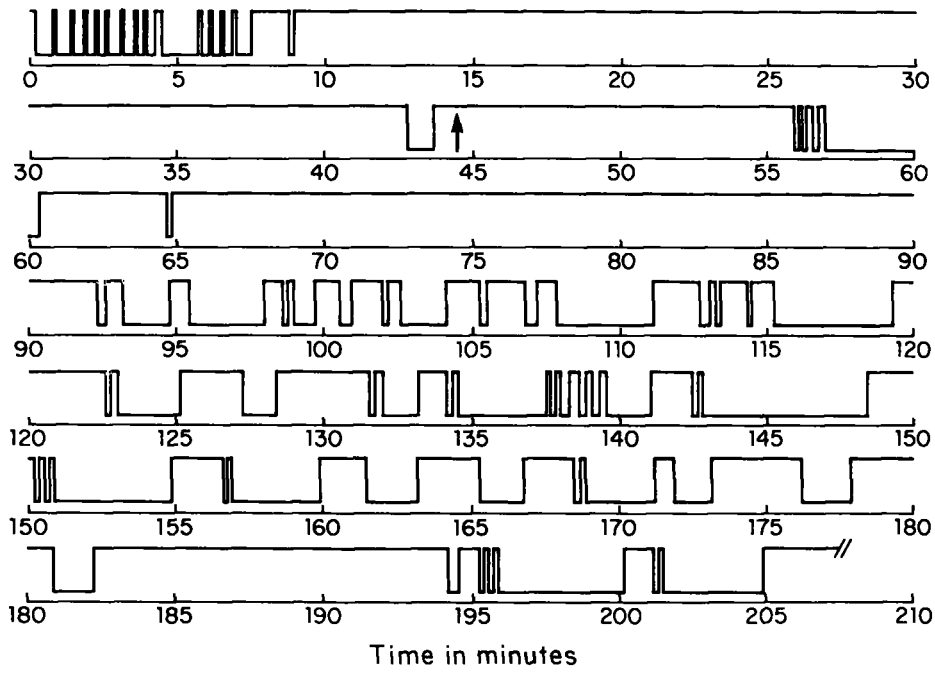

FIGURE 1.—Dive record of the right whale constantly observed for 3.5 hours on 3 March 1986. 44 minutes (arrow): The ship approached to within 10 m of the whale for i.d. photographs and size measurement. 54 minutes: The whale hyperventilated and dove in an area without krill, then swam northward. 92 minutes: The whale began diving on scattered small krill schools while still traveling N and NNW. 140 minutes: The whale stopped and began diving on one large concentration of krill. 182 minutes: The whale rested on the surface, moving its jaws. 194 minutes: The whale began a second feeding bout ca. 400 m further south.

narrow channel. Thereafter the whale ignored the ship and altered course to NNW, still swimming at the surface. The ship pulled ahead of the whale to measure its length and this may have caused the short dive noted at $t = 43$ minutes. However, the whale calmly surfaced again within 10 m of the ship and watched us while we photographed it next to the wooden disk. The whale was 11 m long. The whale then continued to swim at the surface to the NNW. During the period that the whale swam at the surface without diving the average time between breaths was 50.8 seconds ($n = 55$; SD = 10.8). At $t = 54$ minutes the whale began to hyperventilate, took three short dives, lifted the flukes partially clear of the water (false fluking) on the third dive, and then fully raised the flukes on the fourth dive, which lasted 210 seconds. The whale then remained at the surface for about 30 minutes while swimming northward.

This pattern of hyperventilation prior to a long dive occurred before every long dive sequence which was preceded by a surface interval of at least 4 minutes (Fig. 2). We used this criterion to restrict our dive selection for this plot because there is some indication that there is also a brief recovery period involving hyperventilation after long dives. Of the last 19 breaths that were taken during the 90 seconds before the 5 long dives plotted in Figure 2, 18 were less than 30 seconds apart, with a mean interval of 15 seconds ($N = 19$, SD = 7.3). During the time preceding this 90-s hyperventilation period, the whale averaged 1 breath every 48 seconds ($N = 17$, SD = 12.4), not significantly different from the time of 50.8 seconds recorded between breaths during long surface intervals without dives. During hyperventilation, therefore, breathing rate increased by about 3×.

At $t = 92$ minutes we began to record scattered small krill schools on the echosounder and the whale began to dive erratically, with some reasonably long dives, but most quite short. Of 23 dives, 13 (56%) were shorter than 10 seconds; the time averaged for all dives was 75.3 seconds

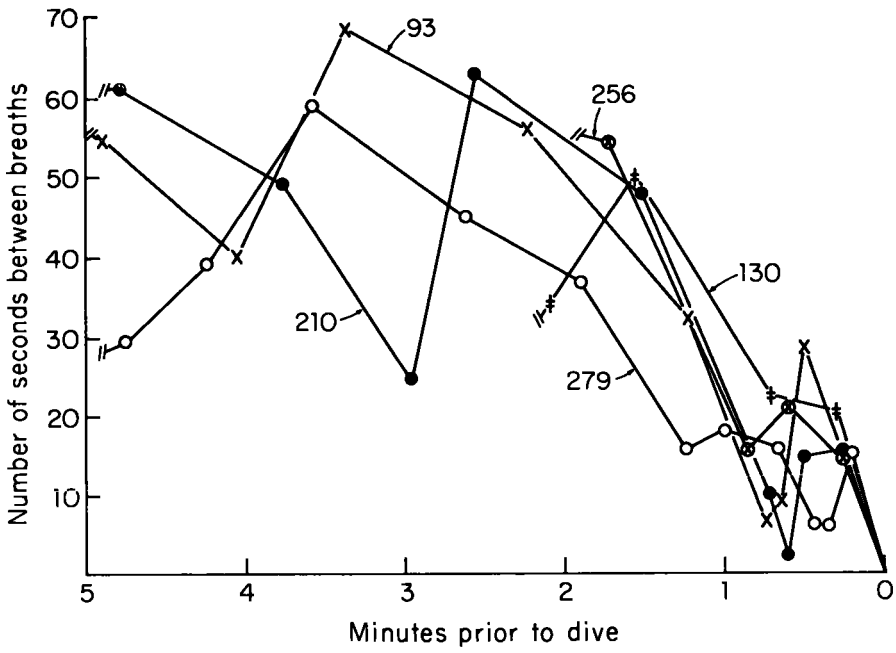

FIGURE 2.—Breath sequences prior to 5 dives lasting from 93 to 279 seconds. During the 90 seconds immediately preceding dives, the mean interbreath interval was 15 seconds. Prior to this 90-s period of hyperventilation the mean interbreath interval was 48 seconds.

(N = 20, SD = 74.6). During this period of erratic diving the whale continued to swim N, then NNW. At about t = 140 minutes the whale stopped traveling NNW and began a series of 10 dives, the second being the longest, followed by successively shorter dives. These dives were followed by rather uniform surface intervals and all 10 lasted significantly longer ($\bar{x}$ = 183.5 seconds, N = 10, SD = 89.2) than the previous mean of 75 seconds. At the end of the dive sequence, at 182 minutes, the whale stopped swimming entirely and floated motionless at the surface, occasionally moving its jaws. This inactivity lasted about 12 minutes and then the whale began a second series of dives. We called these dive sequences, which consisted of regular length surface intervals interspersed with a series of longer dives of progressively decreasing duration, "feeding bouts" because at t = 140 seconds the whale had reached the only major aggregation of krill in the vicinity, as verified by sonic records (Fig. 3). We saw dense schools of krill and isolated krill at the surface from the bow of the ship, and we captured krill in three successive hauls with the 1 m Isaacs-Kidd midwater trawl.

During the first feeding bout the whale slowed from its steady 3-knot swimming speed and moved slowly at about 1 knot, but no longer in any specific direction, finally swimming some 400 m to the south before beginning the second feeding bout. The whale had fed on krill earlier also, because it defecated during the feeding sequence and the feces, as determined by later microscopic examination, were composed entirely of well-digested euphausiids.

The display of a false fluke prior to the high fluke initiating a long dive did not necessarily indicate presence or absence of krill, but when krill were present, it was a highly significant predictor of the length of the dive. In the presence of prey, when the whale showed its flukes once (i.e., did not false-fluke preceding the dive), dive duration averaged 91.2 ± 13.0 seconds (N = 5), whereas when both a false fluke and a high fluke preceded the dive, the dive averaged 234.7 ± 64.4 seconds (N = 7).

In March and April 1986 we saw a total of eight southern right whales. Of these we distinguished four as individuals on the basis of video tapes and photographs of callosities and body markings. One of these whales was the same individual that we had observed in January some 70 miles fur-

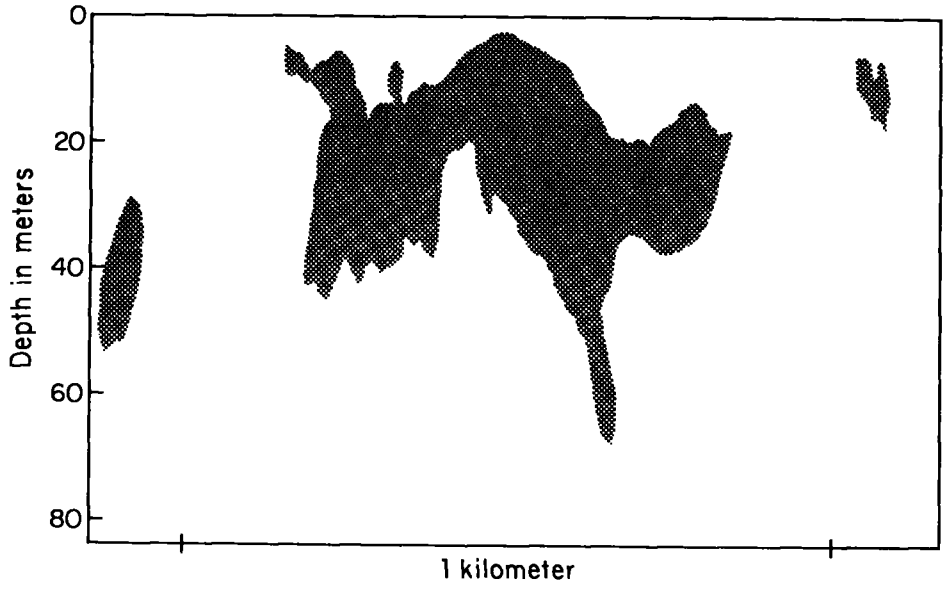

FIGURE 3.—Echogram of krill school on 3 March 1986 on which right whale stopped swimming and began feeding bout.

ther north, as confirmed by comparing video recordings of both sightings. Photographs of these four individuals were subsequently compared with the catalog of southern right whales that overwinter near Peninsula Valdes, Argentina (Payne and Rowntree 1984), but none of the Antarctic individuals were in that compendium of some 623 individuals.

DISCUSSION

Our observations of southern right whales along the Antarctic Peninsula suggest that coastal Antarctica may have been (and may well become again) a regular part of the summer feeding range of the species. These sightings indicate a more extensive distribution in the Southern Ocean than heretofore reported, an extension corroborated by the comparison of recent and historic summer distributional patterns by Ohsumi and Kasamatsu (1986). Southern right whales were hunted almost to extinction in the shallow coastal embayments where they overwinter more than 100 years before whaling began in the Southern Ocean (Harmer 1928; Townsend 1935). It is not surprising, therefore, that there are only a few scattered records of southern rights in Antarctic waters, fluke observations so to speak. During the past 50 years southern rights have been protected, and several demes of southern right whales have increased (Best 1981; Ohsumi and Kasamatsu 1986; Whitehead et al. 1986), and a commensurate extension of the summer feeding range into areas formerly occupied by these whales may be occurring.

It is interesting that none of the 4 individual whales for which we have photographic identifications appear in the catalog of 623 individual southern rights for the Valdes, Argentina breeding population (Payne and Rowntree 1984). We believe that the right whales we encountered in Antarctic waters probably winter elsewhere, perhaps along the Chilean coast, which has been less well surveyed than has the east coast of South America (Cardenas et al. 1986).

Payne (1976) described tail-sailing among the Valdes population of southern right whales and suggested that this may be a form of play behavior. In Antarctic waters this behavior may be a method used to forage on krill. The right whale that we observed tail-sailing had three fur seals in attendance, constantly darting about its head, apparently feeding on the same prey as the whale. Furthermore, tail-sailing occurred next to a grounded iceberg at a specific location that was repeatedly transected by the whale, the only spot in the vicinity where krill were detected on the ship's sonar.

Northern right whales feed by both surface-skimming and subsurface feeding, apparently holding the jaws agape below the surface much like they do when at the surface (Watkins and Schevill 1976, 1979). Surface-skimming by northern right whales that feed on copepods and juvenile euphausiids occurs at speeds of about 3 knots with relatively little turbulence (Watkins and Schevill 1976, 1979). The one southern right whale which we observed surface-skimming, and which was also mentioned in Goodall and Galeazzi (1986), swam at about 8 knots, with an immense amount of turbulence. This whale undoubtedly was feeding on *Euphausia superba*. The extremely high speed of this whale when surface-skimming may be related to type of prey. *Euphausia superba* is a large euphausiid that swims up to 30 cm/second, and it is quite adept at avoiding scuba divers and other dark objects (Hamner et al. 1983; Hamner 1984). It may be that right whales adjust the speed of their surface feeding runs to overcome the swimming speed of the particular prey that they pursue. Fin whales also exhibit differences in breathing and diving rhythms when feeding on euphausiids and on schooled fish (Watkins et al. 1984).

The southern right for which we have a 3.5-h record in 1986 fed exclusively below the surface. It swam for about an hour at the surface almost directly NNW toward the only patch of krill that we had located previously via the echo sounder during repeated transects across the mouth of Andvord Bay. It is not understood how baleen whales locate prey. They might echolocate, they might listen for krill noises, or they might remember where they had prior success and return to the general vicinity and then begin to hunt randomly. Although our data do not allow us to choose among these possibilities, it appears that this particular southern right whale did navigate directly to patches of prey, as suggested by Watkins and Schevill (1979) for northern right whales. However, some subsurface searching probably occurs as well. The whale that we followed for the longest period of time made a reasonably long dive of 210 seconds in the middle of its surface swim toward the krill patch. It apparently did not find anything to eat (nor did the sonar indicate the presence of krill), and it made no more significant dives for about 30 minutes.

When the whale reached an area with small scattered krill schools, its dives were generally short, and the temporal spacing and duration of dives and surface intervals were erratic. When the whale reached a large school of krill it stopped swimming between dives, dives lasted longer, surface intervals between dives became more regular, and successive dives were progressively shorter. After 10 of these dives the whale floated without any swimming movements at the surface for about 12 minutes while occasionally rattling its baleen and slightly lifting its upper jaw.

The whale clearly anticipated its dives. It hyperventilated for about 90 seconds prior to all of the long dives. Hyperventilation is a common precursor to diving in air-breathing vertebrates (Kooyman et al. 1981), but this respiratory pattern apparently has not been reported previously for a baleen whale.

The data that we present in support of this feeding pattern are admittedly modest, consisting of only one continuous 3.5-h data sequence for one individual. Nonetheless, this data set is truly unique and it includes a series of statistically significant changes of behavior at the surface and at depth which are correlated with prey distribution. Since the changes of behavior are real, they merit interpretation. One hypothesis to account for the increase and then the decrease in dive length after encountering prey is that the whale dove to its full capacity in order to maximally exploit an opportunity to feed. With repeated dives its dive capacity may have diminished, producing first long, then shorter and shorter dives (Fig. 1). In contrast, this breathing pattern has not been observed in grey whales, which exhibit a sustained capacity for repetitive, nearly monotonic diving while feeding (Obst et al. in prep.). It is possible that right whales, being more specialized for surface-skimming, become exhausted more readily during sustained diving.

An alternative hypothesis to account for this pattern of behavior is that the whale captured krill with such ease on the first long dive of 348 seconds that a "digestive bottleneck" (Kenward and Sibly 1977) developed; subsequent dives would be progressively shorter because the stomach (or some storage chamber) filled more rapidly than the food could be processed. The long surface interval of immobility followed by a second feeding bout might then represent the time taken to clear such a chamber (e.g., the first of the three stomach pouches) in preparation for the next bout of feeding. If this hypothesis is correct, it implies that once a right whale has found a particularly favorable school of krill, it fills up very rapidly. This interpretation contrasts markedly with a popular impression of great whales as continuous

feeders that harvest prey while swimming lazily through diffuse planktonic resources. Herwig et al. (1984) presented preliminary evidence that microbial fermentation of ingesta may occur in the forestomach of baleen whales, a process which may be expected to limit the throughput rate of food in accordance with continuous-flow, stirred tank reactor kinetics (Penry and Jumars 1987). It is tempting to speculate that the feeding behavior of right whales, among the largest endotherms on earth, may be constrained by a digestive bottleneck analogous to that described for hummingbirds (Karasov et al. 1986), the smallest of endotherms. These hypotheses warrant subsequent testing through more extensive time-budget analyses of right whales and other balaenopterans on their feeding grounds, such as described here and in Watkins et al. (1984).

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NOTES

AN ECONOMETRIC ANALYSIS OF NET INVESTMENT IN GULF SHRIMP FISHING VESSELS[1]

The major capital inputs in the Gulf shrimp fishery are vessels and gear. Early vessels, built mostly of wood, employed drag seines, cast nets, and fixed traps to catch shrimp. Today, much larger and more powerful vessels, equipped with sophisticated fishing gear and accessories, trawl the Gulf of Mexico. The last 20 years has seen a remarkable substitution of steel and fiberglass vessels for wooden vessels. The factors underlying this aggregate investment trend in the Gulf of Mexico (hereafter referred as the Gulf) shrimp fishery, however, have yet to be examined.

Economic analysis of the fishing industry has increased in recent years because of the growing importance of world fish stocks. However, these studies have been focused predominantly at the micro or firm level (Thompson et al. 1970[2]; Wilson et al. 1970; Juhl 1974; Watson 1977; Griffin et al. 1978; Prochaska and Cato 1981). Moreover, accounting for a comprehensive mean of the cost of capital has been ignored in past research efforts. Yet, the cost of capital is likely a major factor in fishing vessel investment decisions in the Gulf shrimp fishery. The long run profitability of the sector and its exposure to financial risk depends, to a large extent, upon its capital structure and fluctuations in the cost of debt and equity capital. Futhermore, this determinent of aggregate investment behavior represents a major channel through which macroeconomic policy actions are transmitted to the Gulf shrimp fishery.

The purpose of this study is to estimate an econometric model of annual real net investment in fishing vessels in the Gulf and to determine the sensitivity of investment decisions in the industry to fluctuations in the cost of equity and debt capital. This study begins by examining the individual factors that affect the expansion of the stock of steel, wood, and fiberglass vessels in the Gulf fleet. The effects of alternative macroeconomic policies on investment expenditure trends in the Gulf shrimp fishery are then studied. The final section of this paper presents some concluding remarks.

Determinants of Net Investment

The aggregate investment model used in this study is based upon the neoclassical theory of aggregate investment behavior. The determinants of the desired capital stock of fishing vessels as well as the relationship between this desired capital stock and net investment behavior of Gulf shrimp fishermen are specified in this section.

Desired Stock of Fishing Vessels

In making investment decisions, competitive firms add to their existing stock of capital as long as the present value of the periodic net cash flows generated by an additional unit of capital exceeds its net purchase price. This condition for any particular type of fishing vessel (e.g., wood, steel, fiberglass) can be stated algebraically as follows[3]:

$$\sum_{t=1}^{\infty} p(\partial X/\partial K_j) - (\partial T_t/\partial K_j) - r(\partial D_t/\partial K_j) - (\partial P_t/\partial K_j)(1+\rho)^{-t} > q_j(\alpha - i_c) \times \left(1 + \sum_{t=1}^{\infty} \partial R_{jt}/\partial K_j\right)(1+\rho)^{-t} \quad (1)$$

where variable p represents the real price fishermen expect to receive per unit of output in the Gulf of Mexico shrimp industry, X represents the quantity of shrimp expected to be harvested, K_j is the real stock of the j^{th} category of fishing vessels, T_t and P_t represent the tax payment and principal payment due in period t expressed in constant

[1]Technical Article No. TA-20803 of the Texas Agricultural Experiment Station, Texas A&M University System. This research was supported in part by the Texas A&M University Sea Grant College Program under Grant No. NA81AA-D-00092.

[2]Thompson, Russel G., R. W. Callen, and L. C. Wolken. 1970. Optimal investment and financial decisions for a model shrimp fishery firm. Unpubl. Rep. Texas A&M Univ., TAMU-SG-70-205.

[3]The variables without any subscripts are expected at the time the investment is made to remain constant over time.

dollars, D_t represents debt outstanding in period t, r is the real rate of interest on debt capital, ρ is the real after-tax opportunity rate of return on equity capital desired by fishermen, q_j is the real price paid for the j^{th} category of fishing vessels at the retail level, α is the proportion of investment financed with equity capital, i_c is the investment tax credit rate, and R_{jt} represents the real level of replacement investment in the j^{th} category of fishing vessels required in period t to offset losses in productive capacity due to wearout.

The entire term on the left-hand side of the inequality sign in Equation (1) represents the present value of the additional net cash flows generated by a permanent addition to the j^{th} category of fishing vessels. It is assumed that both the interest and the principal payments, $(\partial P/\partial K_j)$ and $r(\partial D/\partial K_j)$, vary over time as further expenditures are required to maintain the productive capacity of this addition to the capital stock at its original level. The right-hand side of Equation (1) represents the initial downpayment minus the investment tax credit plus the present value of all future cash outlays required to maintain the stock of the j^{th} category of fishing vessels at its new level.

To maximize the present value of their equity, Gulf shrimp fishermen would continue to add to the stock of the j^{th} category of fishing vessels until Equation (1) holds as an equality. Equivalently, maximization of the present value of owner equity requires that[4]

$$p(\partial X/\partial K_j) = \frac{q_j \rho}{(1 - F_j)} \cdot \frac{\alpha - i_c + Z - A}{(1 - i_Y)} \qquad (2)$$

where F_j represents the present value of the stream of capacity depreciation of the j^{th} category of vessels and i_Y is the average income tax rate. The term Z represents the present value of the stream of after-tax interest payments and principal payments on debt while A represents the present value of the stream of tax depreciation allowances that can be claimed for each dollar of investment as the stock of vessels is maintained at its new level.[5] The right-hand side of this expression thus represents the implicit rental price of the j^{th} category of fishing vessels.

The concept of the implicit rental price of capital has been widely employed in previous studies of investment behavior as a determinant of the capital stock which firms desire to hold (e.g., Coen 1968, 1975; Penson et al. 1981). Equation (2) suggests that the implicit rental price of the j^{th} category of fishing vessels will increase if their purchase price, the cost of debt, and equity capital, or income tax rates increase. These effects, however, will be offset to some extent by an increase in the investment tax credit rate, the deductibility of tax depreciation allowances, and interest expenses.

Let us assume that output in this industry is a function, in part, of the stock of fishing vessels and that this production relationship is of the Cobb-Douglas form. Letting β_j represent the partial production elasticity associated with the stock of the j^{th} category of fishing vessels (K_j), the marginal physical product for these vessels can be expressed as follows:

$$(\partial X/\partial K_j) = (\beta_j(X/K_j). \qquad (3)$$

Substituting Equation (3) into Equation (2), the desired stock of the j^{th} category of fishing vessels at the end of year t can be expressed as follows:

$$K^*_{jt} = \beta_j(pX/c_j)_t \qquad (4)$$

where c_j represents the expected implicit rental price of the j^{th} category of fishing vessels given by the right-hand of Equation (2). Equation (4) implies that the desired stock of j^{th} category of fishing vessels is directly related to the expected real gross income from Gulf shrimp fishing and is in-

[4]Equation (1) as well as the derivation of the implicit rental price of vessels (c) assume that fishermen expect real prices (p) and the marginal physical product of vessels $\partial X/\partial K$ to remain at current levels. These and other assumptions which allow us to treat many components of Equation (1) as consoles are consistent with those employed in Penson et al. (1981) and Coen (1975).

[5]The nominal value of Z (the present value of the stream of after-tax loan payments) in Equation (2) is equal to

$$(1 - i_Y)\Psi \sum_{i=1}^{n} d_i(1 + \phi)^{-i}(1 + \rho)^{-i} + \Psi \sum_{i=1}^{n} (e - d_i)(1 + \phi)^{-i}(1 + \rho)^{-i}$$

while the real value of A (the present value of the stream of depreciation allowances is equal to

$$i_Y(\delta/(\rho + \phi + \rho\phi + \delta))$$

where d_i is equal to the nominal interest payment on a loan of one constant dollar, ϕ is the inflation rate, e is the nominal amortized loan payment on a loan of one current dollar, and δ is the tax depreciation rate given by $2/n$ where n is the service life of the vessel.

versely related to the expected implicit rental price of these vessels. Similar equations could be developed for other inputs used in the shrimp fishing effort.

Desired Net Investment in Fishing Vessels

New fishing vessels are acquired by Gulf shrimp fishermen both to expand their productive capacity and to replace losses in the productive capacity of existing vessels. This partitioning of observed gross investment into net investment and replacement investment for the j^{th} category of fishing vessels can be expressed definitionally as follows:

$$N_{jt} = K_{jt} - K_{jt} = I_{jt} - R_{jt} \tag{5}$$

where I_{jt} represents the level of real gross investment in the j^{th} category of fishing vessels in year t while R_t is the real replacement investment needed to offset annual capacity depreciation of these vessels. The variables K_t and K_{t-1} represent the productive capital stock of the j^{th} category of fishing vessels the end and the beginning of the year, respectively. Given Equations (4) and (5), the following relationship between the desired stock of the j^{th} category of fishing vessels and current real net investment in these durable inputs can be defined:

$$N_{jt} = \theta_j(\mathrm{K}^*_{jt} - K_{jt-1}) \tag{6}$$

where $0 < \theta_j \leq 1$ and where θ_j represents the partial adjustment coefficient that describes the speed of adjustment of actual stocks to desired levels for the j^{th} category of fishing vessels. Substituting Equation (4) into Equation (6) and assuming an adaptive expectations hypothesis for $(pX/c_j)_t$, the following compound geometric expression is obtained:

$$N_{jt} = \theta_j\,\beta_j\lambda(pX/c_j)_t + (1-\lambda_j)N_{jt-1} + \theta_j(1-\lambda_j)K_{jt-2} - \theta_j K_{jt-1} + \mu_{jt} \tag{7}$$

where λ_j is the adaptive expectations coefficient and μ_{jt} represents the error term. Since K_{jt-2} is equal to $K_{jt-1} - N_{t-1}$, Equation (7) reduces to the following estimating equation:

$$N_{jt} = b_{j0} + b_{j1}\,(pX/c_j)_t + b_{j2}\,K_{jt-1} + b_{j3}\,N_{jt-1} + \mu_{jt} \tag{8}$$

where b_0 is the intercept, $b_1 = \theta\ \beta\lambda$, $b_2 = -\theta\lambda$, $b_3 = (1-\lambda)\ (1-\theta)$ and μ_t is once again the random disturbance term. The estimates of the b_1 and b_3 coefficients are expected to be positive while the value of b_2 is expected to be negative.[6] Equation (8) thus represents the general form of the equations to be econometrically investigated in this study.

Data

The time series data used in this study consist of annual observations for each variable in Equation (8) over the 1965-77 period. This time period represents the only period for which investment expenditure information is available.

The productive capital stock of the j^{th} category of fishing vessels is comprised of a series of different vintages of vessels or

$$K_{jt} = I_{jt} + (1-h_{j1})I_{jt-1} + (1-h_{j1}-h_{j2})\mathrm{I}_{jt-2} + \ldots + (1-h_{j1}-h_{j2}-\ldots-h_{jn})I_{jt-n} \tag{9}$$

where h_{ji} is the fraction of the j^{th} category of fishing vessel's original productive capacity lost in the i^{th} year of its service life. The value of h_i is represented by $(1-\phi)^{i-1}$, where $\phi = 2/n$ and n is the assumed service life.[7] In a related matter, the present value of the stream of capacity depreciation of a vessel (F_j) was computed as follows:

[6]The net investment model expressed in Equation (8) can be seen as a part of a simultaneous equation system that includes other investment equations as well as supply equations for all inputs and the production function for the fishing industry. The specification of the complete simultaneous system of equations and measurement of time series data needed to simultaneously estimate the b_i coefficients in Equation (8) are beyond the scope of this study. Since the disturbance terms for this set of investment equations are likely correlated, the seemingly unrelated regression equations estimator was employed. The disturbance terms given by this estimator were also examined for autocorrelation. The estimated rho coefficient in this small sample was shown to be insignificant in all cases. Finally, the predicted rather than actual value of N_{t-1} was used in estimating Equation (8) to address the possibility of correlation between the lagged dependent variable and the disturbance term.

[7]While a geometric decline in productive capacity has been assumed for fishing vessels, recent studies indicate that the productive capacity of equipment and machinery deteriorates at a lower rate in the early period than in latter years. Coen (1975) suggested that equipment and machinery deteriorate as they age, though not necessarily at a geometric rate. For farm tractors, a concave decay pattern represents the best proxy for the capacity depreciation pattern suggested by engineering considerations (Penson et al. 1981). The true pattern which underlines actual capital spending decisions in the fishing industry could not be examined due to inadequate data.

$$F_j = \sum_{i=1}^{x} h_{ji}(1 + \rho)^{-i} \qquad (10)$$

Data from the National Marine Fisheries Service were used as annual observations on the nominal value of gross investment in Gulf fishing vessels (U.S. Department of Commerce 1965-77[8]). These values were deflated to real terms using the industrial price index. The quality of the time series for real net investment in fishing vessels, N_t, depends on how well the annual values of I_t reflect quality changes in vessels over time.

The annual levels of the implicit rental price of vessels (c) were computed using the definition outlined on the right-hand side of Equation (2). Coen (1975) assumed that the real after-tax rate of return desired on equity capital, ρ, is constant over the economic life of the investment. Following the lead of Coen, a value for ρ of 5% was employed in this study.

The real rate of interest on nonreal estate loans at commercial banks, r, along with annual rate of inflation equals the nominal rate of interest on debt capital. Annual values for all these variables were obtained from U.S. Department of Commerce publications. The annual values for the fraction of investment expenditures that are debt financed (ψ) used in computing Z were found by dividing the annual change in total debt in the fishing industry by the annual level of gross investment in durable inputs provided by the National Marine Fisheries Service. The time series for α, the fraction of capital expenditures financed with internal equity capital, was equal to one minus the percentage debt financed $(1 - \psi)$.

Investment tax credit rate, i_c, was equal to 7% during the 1965-68 period, 0% during the 1969-70 period, and 10% during the 1971-77 period. The maximum corporate income tax was assumed to represent i_y for the Gulf shrimp fishery. The double-declining balance method was assumed in determining the present value of the stream of annual tax depreciation allowances in A.

The time series data on prices paid for vessels, a component of the rental price, were measured using cost data collected from shrimp vessel builders. Griffin et al. (1978) have shown that vessel length, material of construction, and year of purchase were the most significant factors determining the price of a vessel. The equation estimated in that study was used to extend available vessel price information over the entire time period covered by this study.

[8]U.S. Department of Commerce. 1965-77. Vessel characteristics data. National Marine Fisheries Service, NOAA, Wash., D.C.

Econometric Results

Statistical as well as economic criteria can be employed to evaluate the estimated equations for the various categories of fishing vessels. The economic criteria include the reasonableness of the elasticities for the economic variables and as well the partial production elasticities implied for the production function.

Empirical estimates of the annual real net investment model for steel, wooden, and fiberglass vessels indicate statistically significant coefficients for all but one of the explanatory variables at the 10% level or less (Table 1). The lone exception was the coefficient associated with the lagged capital stock variable in wooden vessel model, which was not significantly different from zero at less than the 20% level. All the coefficients associated with the explanatory variables have the signs hypothesized earlier in this paper. Finally, the coefficients on the lagged dependent variable satisfy the constraint of being both greater than zero and less than one.

TABLE 1.—Estimated coefficients for the annual net investment model for fishing vessels. Gulf Shrimp Fleet, 1965-77.

Vessel type	Constant (b_0)	$(pX/c)_t$ (b_1)	K_{t-1} (b_2)	N_{t-1} (b_3)
Steel	−95.3895	4.3770	−9.1302	0.6318
		[1](6.21)	(6.23)	(2.34)
Wooden	384.3848	0.1132	−3.1944	0.9089
		(1.79)	(0.93)	(1.21)
Fiberglass	0.3819	0.2990	−0.9529	0.2765
		(5.37)	(1.74)	(2.88)

[1]Numbers in parentheses indicate absolute values of t-statistic.

Economic criteria employed in evaluating the reasonableness of the empirical results and in comparing the investment behavior among vessel types include the partial production elasticity of fishing vessels (β). This elasticity is given by $-b_1/b_2$ which is computed using the estimated beta coefficients in Equation (7). It appears that steel vessels, with a partial production elasticity of 0.479, are highly productive and play an important role in the supply of fish. The fishing sector, unlike other sectors of the economy, depends pri-

marily on one major capital input—vessels. Therefore, the high partial production elasticities recorded for steel vessels and fiberglass vessels (0.314) are no surprise. Even though wooden vessels appear to incur more repair and maintenance costs, attract a lower quality crew, and, for that matter, are less efficient than the other vessel types, the low partial production elasticity of 0.033 is surprising. This low partial production elasticity may have been caused by the fact that the instrument for N_{t-1} in the wooden vessels equation used to address the issue of the relationship between the lagged dependent variable and the error term did a poor job of explaining N_{t-1}.

An examination of the elasticities associated with the $(pX/c)_t$ term, computed at the mean, reveals that real net investment in steel vessels is the most sensitive to changes in prices, interest rates, taxes, and the other factors captured in this variable. An elasticity of 7.28 associated with this economic variable was computed for steel vessels. This means that a 1% change in the $(pX/c)_t$ variable causes real net investment in steel vessels to change by 7.28%. This high investment response to changes in these economic relationships could be attributed to the fact that steel vessels, by far the most productive (as evidenced by the high partial production elasticity reported earlier), are the most durable and the most capital intensive. The elasticity associated with the $(pX/c)_t$ term in the fiberglass and wooden vessel equations were 5.35 and 3.11, respectively. This would suggest that macroeconomic policy actions would have a substantially greater effect on real net investment in steel vessels than, say, wooden vessels.

Impact of Changes in Cost of Capital

The impact of high real interest rates on the growth of selected sectors in the economy has been of great concern in the 1980s. The sensitivity of annual real net investment in fishing vessels to changes in the real rate of interest is examined in this section by simulating the estimated equations under annual real rates of 5 and 10%. In the short run (3 years), an increase in the real rate of interest on debt capital from 5 to 10% would cause real net investment in fishing vessels to decrease by 3.04%. Annual real net investment in these fishing vessels would decrease by 15.88% in the long run. As the real rate of interest on debt capital increases, it becomes more difficult to justify the purchase of additional vessels owing to their rising marginal factor cost. Given the fact that 67% of the cost of new fishing vessels is normally financed with debt capital, it is not surprising that rising real interest rates on debt captial have a significant negative effect on the long run expansion of the Gulf fleet.

The real cost of equity capital, which reflects the opportunity cost of the fisherman's own funds, has a less dramatic effect on annual real net investment in fishing vessels. This can be attributed to the fact that only 33% of the cost of new fishing vessels are financed with equity capital. The short run impact of an increase in the real cost of equity capital from 5 to 10% translates into only a 1.76% decrease in annual real net investment in fishing vessels in the short run. This same change in the cost of equity capital would result in a 12.32% decrease in annual real net investment in the long run.

Summary and Conclusions

This study evaluated aggregate investment behavior by fishermen for steel, wooden, and fiberglass fishing vessels in the Gulf of Mexico shrimp fishery and examined the implications of changes in the cost of acquiring debt and equity capital on the industry's investment response. This study showed statistical justification for the theoretical model of aggregate investment behavior for all three vessel types.

It is quite evident that the cost of capital plays an important role in influencing the investment decisions in the Gulf shrimp fishing industry. Macroeconomic policies that lead to high real interest rates depress real net investment in this fishery. Capital expenditures for steel vessels are the most sensitive to changes in real interest rates while wooden vessels are the least sensitive. While low real interest rates are desirable for stimulating investment activities in the general economy, they would add to the overcapitalization problem which currently exists in the Gulf shrimp fishing industry. Finally, this study underscores the need to reinitiate efforts to collect data on gross investment expenditures for different categories of fishing vessels in the Gulf fleet.

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APPENDAGE INJURY IN DUNGENESS CRABS, *CANCER MAGISTER*, IN SOUTHEASTERN ALASKA

The Dungeness crab, *Cancer magister*, is commercially important along the western coast of the United States. Like many decapod crustaceans, it can autotomize and regenerate appendages to heal wounds and limit injury.

Studies of appendage injury may be useful in assessing the physical condition of crustacean populations and the impact of fishing on commercially important species. Incidences of appendage loss in the field have been reported for species of crabs other than *C. magister* (McVean 1976; McVean and Findlay 1979; Needham 1953). Appendage loss was studied in adult Dungeness crabs in Washington (Cleaver 1949) and Oregon (Waldron 1958) and for juvenile crabs in the Columbia River estuary (Durkin et al. 1984).

In this study we examined adult Dungeness crabs in southeastern Alaska to determine the incidence of missing, regenerating, and damaged appendages. Temporal incidence of appendage injury was compared to the molting and mating periods of the crabs and to the commercial fishing season for Dungeness crabs.

Materials and Methods

Adult Dungeness crabs were collected from Icy Strait and the Excursion Inlet fjord near Glacier Bay, AK (lat. 135°30'N, long. 58°25'W), from May through November 1984-85. Data were obtained by monthly surveys of commercially caught crabs. Crab pots (Waldron 1958) were set at depths of 7 to 20 m and remained in the water for 3 to 11 days. All crabs were held in live tanks (<24 hours) before they were measured on board ship. In southeastern Alaska, pots are equipped with escape rings to permit release of crabs with carapace widths <165 mm, but sublegal-sized crabs are often found in the catch.

Carapace width (excluding the 10th anterolateral spines), wet weight, and sex were recorded for each crab. Carapace condition was graded as soft-shell (recent molt), new-shell, worn-shell, or skip-molt (Somerton and Macintosh 1983). The number and identities of missing, damaged, or regenerating chelipeds and walking legs were recorded. An appendage with a cracked cuticle or missing dactyl was considered damaged. Appendages smaller in length and diameter than intact appendages were designated regenerating. Combined missing, damaged, and regenerating appendages are referred to as injured appendages.

Interrelationships between variables were determined with Pearson correlations (SAS 1985). Means were compared with Student's t-tests, and chi-square analyses were used to determine if multiple autotomies occurred by chance (Steel and Torrie 1960). Data are presented as means ± 1 standard error of the mean.

Results

Males comprised 65% and females 35% of the 878 Dungeness crabs examined. Average carapace widths were 169 ± 0.6 and 159 ± 0.7 mm for males and females, respectively. Wet weights were $1{,}102 \pm 9$ g for males and 884 ± 14 g for females. The greatest number of female crabs was caught in July, and the greatest number of males in August.

Seventy-five percent of the crabs were intact, with no appendage injuries. Twenty-five percent of all crabs had injured limbs; 18% had missing, 5% had regenerating, and 2% had damaged appendages. No relationship existed between carapace width and appendage injury.

Most of the Dungeness crabs sampled were in the worn-shell condition (67%). Twenty-eight percent of all crabs were new-shelled. Only 1% were soft-shelled and 4% were skip-molts. Correlations between carapace condition and appendage injury were not significant.

No significant differences existed in appendage injury between male and female Dungeness crabs. Injuries were bilaterally symmetrical except for the 3d walking leg which was missing more frequently on the left side ($P < 0.05$). Considering only those crabs with missing legs, a total of 246 legs were missing with a mean of 1.5 ± 0.1 missing legs/crab. Ninety-seven crabs had legs missing on the right side and 98 had legs missing on the left side. The maximum number of missing legs per crab was 5. Sixty percent of the crabs had 1 leg missing, 20% had 2 missing legs, and 12% were missing 3 or more legs. Of the crabs with missing legs, 63% were males and 37% were females.

Forty Dungeness crabs had regenerating legs, with a mean of 1.2 ± 0.1 regenerating legs per crab. Sixty percent of those crabs had 1 regenerating leg, 10% had 2 regenerating legs, and 3% had 3 or more regenerating legs. The maximum number of regenerating legs per crab was 4. Of the crabs with regenerating legs, 73% were males and 27% were females.

Seventeen crabs had damaged appendages with a mean of 1.1 ± 0.1 damaged appendages/crab. Of the crabs with damaged appendages, 82% were males and 18% were females.

The observed number of Dungeness crabs with 2 or more missing appendages was significantly higher ($P < 0.01$) than expected for both sexes, indicating that appendage loss was not due only to chance.

Appendage injury was significantly correlated with date, with more injuries occurring later in the year. The number of Dungeness crabs with missing appendages was significantly correlated with date for both males and females ($P < 0.01$). The lowest percentage of crabs with injured appendages occurred in July (4.8%, both sexes combined) and increased to a maximum of 34.3% in November. The percentage of male crabs with regenerating appendages did not vary significantly over time and was about 6% for all months. However, the percentage of female crabs with regenerating legs increased from 0% in May to 10.5% in November ($P < 0.01$). Male crabs with damaged appendages increased from 0% to 8.5% from May to October ($P < 0.05$) and then decreased to 1.7% in November.

Chelipeds and 1st and 4th walking legs were injured most frequently. The hierarchy for frequency of injury for female crabs (chelipeds > 4th walking legs > 1st, 2d, and 3d walking legs) differed slightly from the hierarchy for males (chelipeds > 1st walking legs > 4th walking legs > 2d and 3d walking legs). Months in which high percentages of crabs had injured chelipeds also had high percentages with injured 1st (males) and 4th (females) walking legs (Fig. 1).

The temporal incidence of appendage injury in Dungeness crabs was compared to life history events and to the commercial crab fishing season in southeastern Alaska (Fig. 2). The season opened 15 June and closed 15 August, reopened 1 October and closed 28 February 1986. Appendage injuries were low in July and increased 157% from July to August, a period of simultaneous molting, mating, and fishing. An additional increase in appendage injury of 43% occurred in October, even though the fishery was closed from 16 August to 30 September.

Discussion

Pot samples are biased towards larger sized Dungeness crabs because of the size of the mesh on the pot and the presence of two escape rings with diameters of 11 cm. However, 62% of the crabs collected for this study were either male crabs with carapace widths <165 mm or were females. Very few soft-shell crabs were caught, even though molting was occurring during part of the sampling period. Our dependence on commercial crabbers for data collection restricted us to sampling mostly during the open fishing season when most of the crabs were not in the soft-shelled condition.

Twenty-five percent of the Dungeness crabs sampled in southeastern Alaska had appendage injuries. In other studies of Dungeness crabs in Washington, Oregon, and the Columbia River estuary, 18%, 32%, and 62%, respectively, of the crabs were injured (Cleaver 1949; Waldron 1958; Durkin et al. 1984). The crabs examined in our study were held for up to 24 hours in crowded tanks on board ship before being measured and

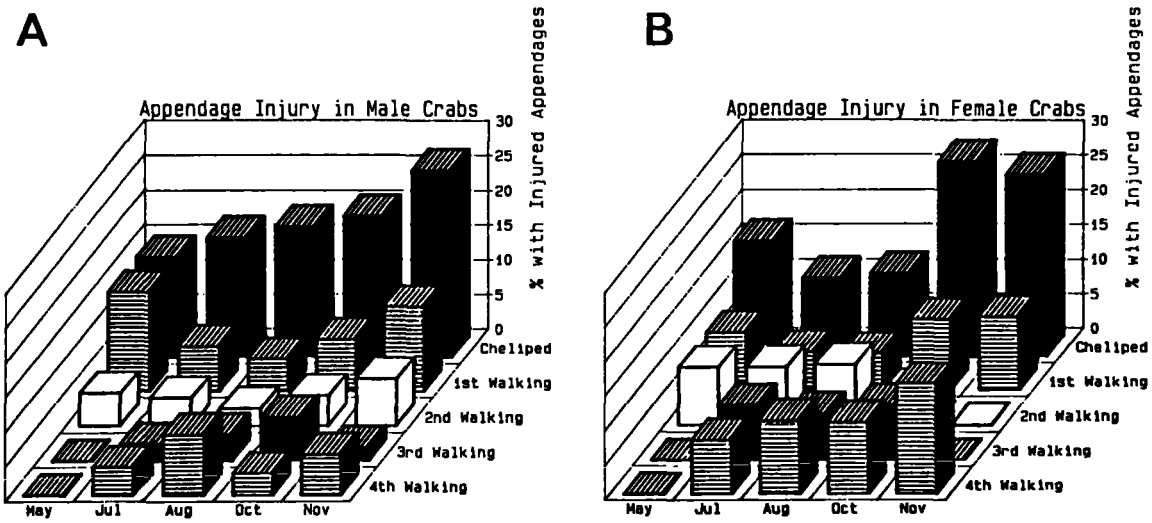

FIGURE 1.—Monthly percentages of male (A) and female (B) Dungeness crabs with injured (missing + regenerating + damaged) chelipeds and walking legs.

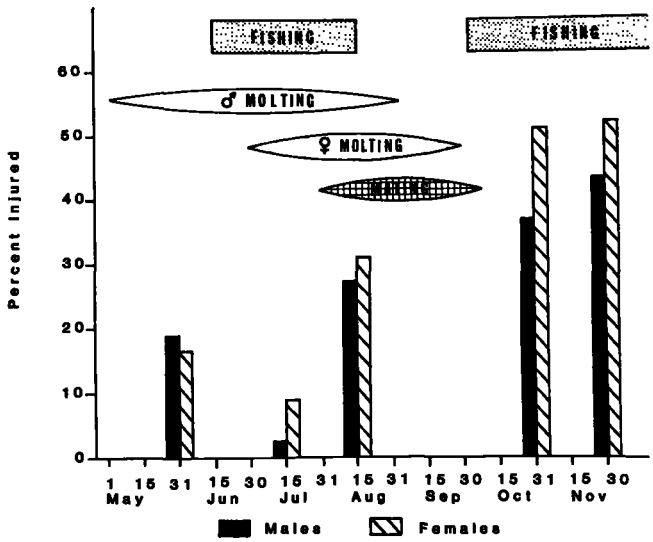

FIGURE 2.—Temporal relationships of percentages of male and female Dungeness crabs with injured (missing + regenerating + damaged) appendages to the crabs' molting and mating periods and the commercial crab fishing season in southeastern Alaska.

were sometimes observed grasping other crabs, but very few autotomized limbs were found in the tanks.

The estimate of appendage injury may be low if Dungeness crabs with injured appendages were less likely to enter pots than intact crabs. In another study, the observed number of *Carcinus maenas* missing 2 or more legs was higher than expected if multiple autotomies occurred by chance, which was interpreted to mean that injured *C. maenas* enter pots as readily as intact crabs (McVean 1976). Because there were more Dungeness crabs with 2 or more missing legs in our collections than would be expected if multiple

autotomies occurred by chance alone, our data could be similarly interpreted to suggest that Dungeness crabs with injured appendages showed little decrease in pot-entering ability and that our estimate of injury was accurate. For this interpretation of the chi-square results to be valid, one must assume that all injuries occurred before the crabs entered pots and that injury did not occur within the pots.

Appendage injury in Dungeness crabs was bilaterally symmetrical except for the 3d walking leg. Interestingly, Easton (1972) demonstrated that 3d walking legs of *Hemigrapsus oregonensis* were the most easily autotomized. In other studies, both bilateral symmetry and asymmetry have been reported for different species of crabs (Durkin et al. 1984; Needham 1953). Asymmetrical appendage loss has been associated with crabs that move predominantly in one direction, while symmetrical leg loss occurs in crabs that move randomly (Needham 1953).

The chelipeds, followed by the 1st and 4th walking legs, were most vulnerable to injury. Limb loss has been correlated in other studies with degree of exposure of the limb; the outermost limbs, the longest limbs and limbs with postures that afford little protection are most frequently lost (Needham 1953). Anterior limbs are lost more frequently than posterior limbs (Needham 1953). The chelipeds are the most anterior and one of the most exposed appendages on Dungeness crabs and are frequently used in aggressive threat postures. After loss of chelipeds, the 1st walking legs remain as the most anterior, exposed limbs and therefore, the most vulnerable. The 4th walking legs are the most posterior and also very exposed limbs on an intact crab.

A significantly greater number of Dungeness crabs with 2 or more missing legs was observed than expected if multiple autotomies occurred by chance, indicating an increased susceptibility to subsequent appendage loss after initial injury (Needham 1953; Easton 1972).

The correlations between appendage injury and date were significant but may not be biologically important. Although these correlations were significant, the r^2 values (square of the coefficient of variation) were low. Increased appendage injury later in the year may be related to other factors. Soak times, the length of time pots were left in the water, were longer later in the year. Dungeness crabs may cannibalize other crabs while confined in pots (Waldron 1958). There may also be delays between time of injury and subsequent autotomy and regeneration. Regeneration of legs in Dungeness crabs is usually completed after 2 or 3 molts (Cleaver 1949).

Over the sampling period, only 5% of all crabs had regenerating appendages while 18% had missing appendages. The discrepancy may be due to increased mortality of the crabs following injury (McVean and Findlay 1979), or by the efficient, yearly removal of legal-sized, injured crabs by the commercial fishery.

When temporal incidence of appendage injury was compared with the opening and closing of the commerical Dungeness crab fishing season, considerable appendage injury occurred when the fishery was closed. Closure of the fishery traditionally occurs during the crabs' mating period, when a high percentage of soft-shelled female crabs are present in the population. There was, however, some overlap in late July and early August in fishing, molting, and mating. Excluding damage by humans, potential causes of appendage injury are aggression between males competing for females, the cheliped-to-cheliped mating embrace of Dungeness crabs that can last up to a week, cannibalism, and the increased vulnerability of females which molt prior to mating (Butler 1960; Durkin et al. 1984). Damage to Dungeness crabs can also result from other fishing gear such as trawls (Reilly 1983), but no other commercial fisheries occurred in the study area while the Dungeness crab fishery was closed.

The results of our studies indicate that Dungeness crabs in southeastern Alaska are in comparable condition to adult populations of Dungeness crabs examined in Washington and Oregon, in terms of appendage injury. Further studies are needed to investigate the effect of appendage injury on survival of Dungeness crabs and the contribution of handling injury and mortality of crabs in the commercial fishery.

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REEXAMINATION OF THE USE OF OTOLITH NUCLEAR DIMENSIONS TO IDENTIFY JUVENILE ANADROMOUS AND NONANADROMOUS RAINBOW TROUT, *SALMO GAIRDNERI*[1]

Otoliths are a potential source of taxonomic characteristics for identifying stocks of fish (Ihssen et al. 1981). Differences in dimensions of the otolith nucleus have provided a basis for separating winter from summer races of steelhead, anadromous rainbow trout, *Salmo gairdneri*. In addition, otoliths provided data from which to distinguish steelhead from resident nonanadromous forms as well (McKern et al. 1974; Rybock et al. 1975). Neilson et al. (1985) studied the development of sagittal otoliths in resident rainbow trout and steelhead from south-central British Columbia, and identified sources of variability in the size of otolith nuclei. However, they were unable to find morphometric differences between the two forms of trout. They concluded that the usefulness of dimensions of the otolith nucleus for separating steelhead from resident rainbow trout was much more limited than that suggested by Rybock et al. (1975) for rainbow trout in the Deschutes River, Oregon.

The difference in mean length of the otolith nuclei between the rainbow trout studied by Rybock et al. (1975) and those studied by Neilson et al. (1985) suggested either population differences or differences in defining the nuclear boundary. These disparate results, which led to opposite conclusions, limit the usefulness of measurements of otolith nuclei for the racial identification of juvenile rainbow trout until the source of these differences is better understood. Consequently, to determine whether juveniles of the two forms could be distinguished by differences in dimensions of otolith nuclei, we measured the nuclei in sagittae from steelhead and resident rainbow trout collected from the same Deschutes River, OR, locations used by Rybock et al. (1975). We used the definitions proposed by Rybock et al. and by Neilson et al. (1985), and compared our measurements for the two forms with each other and with published values.

Methods

Resident rainbow trout and steelhead were col-

[1]Oregon State University Agricultural Experiment Station Technical Paper No. 8279.

lected from three locations in the Deschutes River, OR. Resident rainbow trout, which were collected from the main stem near the mouth of Nena Creek in March 1985, were mature and smaller (280–450 mm FL) than the steelhead, and, based on analyses of scales and otoliths (McKern et al. 1974), had never entered saltwater. Juvenile progeny of steelhead were collected from Round Butte Hatchery on the Deschutes River in 1984. Wild juvenile rainbow trout (<200 mm FL) of unknown parental origin were collected in 1984 and 1985 from Bakeoven Creek, an important spawning tributary for steelhead in the Deschutes River.

Sagittae removed from rainbow trout were stored in 90% ethanol for up to two months. Before they were viewed, one otolith from each pair was mounted (concave face up) with epoxy on a glass slide. The back of the slide was blackened with indelible ink. The otolith was ground by hand with 600 grit wet sandpaper and periodically inspected under a light microscope at 100× until the microstructure of the nucleus, as described by Neilson et al. (1985), was visible. The otolith was rinsed with 5% HCl for several seconds to remove scratches and improve resolution.

To reduce bias, we coded each slide with a random number and ordered the slides sequentially for viewing. Otoliths were examined with a Zeiss[2] dissecting microscope at 125×. A camera lucida attachment enabled us to use a computer digitizer to measure three dimensions of the otolith. In measuring length and width of the central nucleus, we used the first growth increment encircling all the central primordia, which was the nuclear boundary defined by Neilson et al. (1985). In addition, we measured the maximum length along the longest axis through an area defined by the first metamorphic check, a narrow hyaline ring surrounding an opaque ring with a hyaline center, to replicate the measurements of Rybock et al. (1975).

We used analysis of variance (ANOVA) to test for significant differences in each dimension of the otolith nuclei among groups in our study. Where adequate data were available, we tested for significant differences between groups in our study and similar groups described by Rybock et al. (1975) and Neilson et al. (1985) for mean dimensions of otolith nuclei. Neilson et al. (1985) showed that the mean length of otolith nuclei for rainbow trout incubated at 6.5°C was significantly less than those for trout incubated at 9.5° or 15.0°C. Because of this discrepancy, we evaluated the potentially confounding effects of incubation temperature on the comparisons of otolith dimensions between our samples and those of Rybock et al. (1975), by testing the hypothesis that water temperatures during 1967–69 were higher than those during 1982–83. We used a paired t-test of average daily water temperatures recorded by the U.S. Geological Survey on the 1st and 15th day of each month from 1 January to 1 August during 1967–69 and 1982–83 (U.S. Department of the Interior Geological Survey 1967, 1968, 1969, 1982, 1983). These dates represent the incubation periods for most of the resident rainbow and steelhead trout sampled in our study and by Rybock et al. (1975). Incubation temperature for steelhead at Round Butte Hatchery is from hatchery records. We estimated spawning and incubation periods for resident rainbow and steelhead trout on the basis of reports of the Oregon Department of Fish and Wildlife (Fessler 1972) and personal observations.

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

Results

For each dimension, we failed to reject the hypothesis ($\alpha = 0.05$) that rainbow trout collected from different populations for our study had otolith nuclei of the same size (Table 1). Therefore, we concluded that these dimensions could not be used to discriminate between the resident and steelhead forms of rainbow trout sampled in our study.

Water temperatures during 1967–69 were slightly greater than those during 1982–83 ($t = 2.03$, df = 14, $P = 0.03$). Mean difference between the two periods was 0.8°C. Spawning dates for resident rainbow trout and steelhead differ; steelhead spawn from January to April and resi-

TABLE 1.—Means, standard errors (in parentheses), and sample size for three otolith dimensions in resident rainbow trout and steelhead from three Deschutes River populations.

Populations compared	No. of fish	Dimensions of nuclei: Nucleus length (mm)	Nucleus width (mm)	Check length (mm)
Resident rainbow trout	44	0.173 (0.006)	0.070 (0.003)	0.323 (0.012)
Hatchery steelhead	30	0.190 (0.006)	0.070 (0.002)	0.349 (0.009)
Suspected wild steelhead	32	0.178 (0.006)	0.069 (0.002)	0.312 (0.007)

dent rainbow trout spawn from May to mid-July (Fessler 1972). Mean water temperature during the period of steelhead egg incubation was 8.4°C for 1967–69 and 7.6°C for 1982–83. Mean water temperature during the period when resident rainbow trout eggs were incubating in the main stem of the river was 12.6°C in 1967–69 and 11.9°C in 1982–83. Incubation temperature for steelhead at Round Butte Hatchery was 10°C and did not vary.

The dimensions of otolith nuclei from resident rainbow trout and steelhead in our study were indistinguishable from those in fish from British Columbia. No significant difference ($\alpha = 0.05$) in mean length of otolith nuclei existed between the British Columbia steelhead incubated at 9.5° or 15°C and suspected wild steelhead from Bakeoven Creek or Round Butte Hatchery steelhead incubated at 10°C. Among resident rainbow trout, the mean length of otolith nuclei for fish from the Deschutes River was also not significantly different from that for fish from British Columbia incubated at 9.5° or 15°C. Because Rybock et al. (1975) did not provide variances, we were unable to test the hypothesis that means from our study coincided with theirs. However, mean length and width of otolith nuclei in our study were 29 and 55% less, respectively, for resident rainbow trout and 49–70% less, respectively, for steelhead than those studied by Rybock et al. (1975).

Discussion

The similarity of our results to those of Neilson et al. (1985), who used similar methods, might be expected for different populations under similar genetic and environmental control. The disparate results of our study and that of Rybock et al. (1975) for the same populations after little genetic change (based on comparisons of unpublished, biochemical genetic data for these populations from 1972 to 1974 and 1984 to 1986) and little environmental change partly reflected the use of different definitions for the nucleus. We defined the nuclear boundary as the first growth ring surrounding all the fused primordia, whereas Rybock et al. (1975) defined the nucleus as the hyaline area in the center of the otolith that is bounded by a metamorphic check formed at hatching; they resolved the check by rendering the otolith with HCl. We also measured the length of the check surrounding the nucleus, as defined by Rybock et al. (1975), which we found either to correspond with the area enclosed by the first check or to increase in density of growth increments surrounding both the central and rostral primordia. The close similarity between our estimate for Round Butte Hatchery steelhead (0.349 mm) and the mean calculated by Rybock et al. (1975) for steelhead (0.354 mm) suggested similar checks. It is unclear, however, why values for resident rainbow trout for this dimension and the results of tests to discriminate races differed between the two studies. Rybock (1973) noted that the nuclear check could not be distinguished in 29% of the otoliths and that the use of HCl may have caused the frequent confusion between the metamorphic check and other groups of daily growth rings. The grinding and polishing of otoliths greatly reduce this source of error. Neilson et al. (1985) also discouraged the use of metamorphic checks as boundaries because the causal links between checks and developmental events, such as hatching, have not yet been established.

Neilson et al. (1985) demonstrated that nuclear length increased significantly with increase in incubation temperature from 6.5° to 9.5°C but not from 9.5° to 15°C. Although average water temperatures in the Deschutes River were 0.8°C lower during 1982–83 than in 1967–69, it is unlikely that such differences completely explain the greater estimates of mean length and width of otolith nuclei in the earlier study by Rybock et al. (1975). Rybock et al. (1975) calculated mean nuclear lengths and widths of 0.354 and 0.230 mm for steelhead and 0.243 and 0.154 mm for resident rainbow trout in the Deschutes River. Our estimates were 29–70% less than their estimates for a 0.8°C difference; whereas under controlled conditions in British Columbia, mean nuclear length for resident rainbow trout at 6.5°C was 18% less for resident rainbow trout and 21% less for steelhead than the nuclear length for fish incubated at 9.5°C, a difference of 3°C (Neilson et al. 1985).

Comparisons of otolith nuclear dimensions between resident rainbow trout and steelhead incubated at similar temperatures would establish whether significant differences exist for these measurements between the two races from the Deschutes River. The use of a common definition of nuclear boundaries would allow better comparisons between studies. However, given the disparate results of our study, which were similar to the results of Neilson et al. (1985), and the original study for steelhead and resident rainbow trout in the Deschutes River, as well as our failure to discriminate between races using both nuclear definitions proposed by Neilson et al. (1985)

and Rybock et al. (1975), we believe that population differences do not explain the differences in results between the studies of Rybock et al. (1975) and Neilson et al. (1985). Furthermore, our study provided strong evidence to support the conclusion of Neilson et al. (1985) that the usefulness of measurements of otolith nuclei to identify sympatric juvenile progeny of resident rainbow trout and steelhead reared in the wild may be limited.

Acknowledgments

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AGE-SPECIFIC VULNERABILITY OF PACIFIC SARDINE, *SARDINOPS SAGAX*, LARVAE TO PREDATION BY NORTHERN ANCHOVY, *ENGRAULIS MORDAX*

To a large degree interannual variability in recruitment determines the size of pelagic fish populations. Recruitment to the Pacific sardine, *Sardinops sagax*, population off California varies from year to year over several orders of magnitude and is unrelated to spawning stock size (Murphy 1966; MacCall 1979). Variable mortality rates in the first year of life must determine year-class strength, although the sources of this variability are unknown. Mortality rates in the earliest stages are size specific with highest rates in the egg and yolk-sac stage (Ahlstrom 1954; Butler 1987) and may contribute to variability in year-class strength (Smith 1985).

The sources of mortality of sardine larvae have yet to be investigated. In other pelagic larvae, mortality is due to either starvation or predation, and starvation is significant only during the brief period after the onset of feeding (O'Connell 1980; Hewitt et al. 1985; Theilacker 1986; Owen et al. 1987). In sardines, significant mortality occurs during the egg and yolk-sac stages (Ahlstrom 1954) and this mortality can only be due to predation. Variable mortality in older larval and juvenile sardines may also contribute to variability in recruitment, and this mortality, as in other fishes, may also be due to predation (Hunter 1984).

The objective of this paper was to determine the size-specific vulnerability of Pacfiic sardine larvae to predation by adult northern anchovies, *Engraulis mordax*. The vulnerability of cape anchovy and northern anchovy larvae to

cannibalism has been investigated by Brownell (1985) and Folkvord and Hunter (1986) and found to be an important source of mortality. In this paper the vulnerability of sardine larvae will be compared with that of anchovy larvae and differences in the biology of sardines and anchovies will be discussed.

Our approach was to observe the avoidance behavior of Pacific sardine larvae in response to predatory attacks by northern anchovy adults. Adult northern anchovy were chosen as a predator because the northern anchovy was the most abundant pelagic fish in the California Current region during the waning years of the sardine fishery and because its planktivorous diet includes fish eggs and larvae (Loukashkin 1970; Hunter and Kimbrell 1980).

Materials and Methods

Experimental Fishes

The Pacific sardine larvae used in the experiments were reared from eggs spawned in the laboratory. Adult Pacific sardines were collected off San Diego and held in 175 m^3 aquarium for six months. Males and females with developing gonads were isolated in spawning tanks and injected with 250 mg human chorionic gonadotropin and on the following day injected with 200 units pregnant mare serum and 20 mg salmon pituitary extract. On the third day fertilized eggs were collected from the spawning tank. Larval rearing procedures follow those described by Hunter (1976). Temperature in the rearing tanks was maintained at 21°C.

Apparatus and Procedures

Experimental apparatus and procedures were the same as those described by Folkvord and Hunter (1986) but will be briefly outlined here. Experimental predators were two groups of 5 adult northern anchovy (range of standard lengths 8.4–9.2 cm). Predators were maintained in two rectangular fiberglass tanks (0.75 × 2.15 × 0.83 m = 1.35 m^3) and fed adult brine shrimp except on days of experimental observation. Seawater was supplied continuously to the tanks except during experiments. The temperature in the observation tank ranged from 16.2° to 22.8°C (mean = 20.1°C). Two 100 W incandescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosing a window on one side of the tank provided a darkened observation chamber.

Each trial consisted of the encounter of three prey with the predators. Prey were introduced into the observation tank with a clear glass beaker. Initial feeding behavior of the predators is quite variable but becomes less variable as the predators become accustomed to prey in the tank. For this reason, prior to each experiment adult *Artemia* were introduced as prey for five consecutive trials to standardize predator behavior. After the preliminary trials with *Artemia*, three trials with sardine larvae were alternated with one trial with brine shrimp until 18 trials with sardine larvae were completed. Each experiment was concluded with a trial of brine shrimp to test for satiation.

The number of observations for each larval size class was the total number of predator-prey interactions observed among larvae in that size class. The mean standard length was determined from 20 larvae sampled randomly from the rearing tank on the day of each behavior experiment. The numbers of observations for each size class (mean SL) were 8.0 mm, 41; 11.3 mm, 51; 12.1 mm, 114; 12.7 mm, 46; 14.1 mm, 81; 17.6 mm, 104; and 19.6 mm, 69. Experiments were not extended to larger sizes due to insufficient numbers of larvae.

Classification of Behavior

Prey behavior was scored only when the predator attacked a prey. Four measures of predator-prey interactions were calculated: predator attack distance, the distance from which the predator responded to the prey and initiated its attack; frequency of avoidance response; frequency of escapes; and predation rate (percentage of larvae captured during the 5-min trials). An avoidance response was a change in speed or trajectory of a larvae before the predator had completed its attack by closing its mouth. An escape was defined as a larval response in which the predator failed to capture the larvae in a single attack. Typically adult anchovy make a single attack on a prey item and do not pursue a prey that escapes (Folkvord and Hunter 1986) but rather continue searching the tank. Thus attacks on one prey item were recorded twice if the first attack was unsuccessful. Although predator attack distance was recorded, this measurement is highly subjective and comparison with the measurements of other observers is suspect. We did not analyze predator attack distance for this reason.

To compare response and escape behaviors of Pacific sardine with those reported by Folkvord and Hunter (1986) for northern anchovy at similar stages of development, mean lengths were converted to ages using field growth rates back-calculated from otolith increment widths for each species. Confidence limits of the percentage of larvae responding or escaping attack were estimated assuming the binomial distribution.

Results

Probability of Response to Attack

The youngest larval stages of both sardine and anchovy were the most vulnerable to predation. Only 17% of 8 mm sardine larvae (smallest size tested) responded to attack by adult anchovy. With increasing size more sardine larvae responded to attack. At 20 mm, the largest size tested, 61% of the larvae responded to attack. The response rate of Pacific sardine larvae was consistently lower than that of northern anchovy larvae of similar lengths (Fig. 1). Although this difference in responsiveness could be due to differences in the observer, it may also be explained by the difference in age of anchovy and sardine at the same length. Sardine larvae are about 6.2 mm when they begin feeding (age = 5 days from fertilization at 17°C), whereas first-feeding anchovy larvae are only about 4.3 mm (age = 5 days from fertilization at 17°C) (Zweifel and Lasker 1976). Sardine larvae also grow faster than anchovy larvae at the same temperature (Butler and Rojas de Mendiola 1985). Thus, sardine larvae are younger at a given size than anchovy larvae.

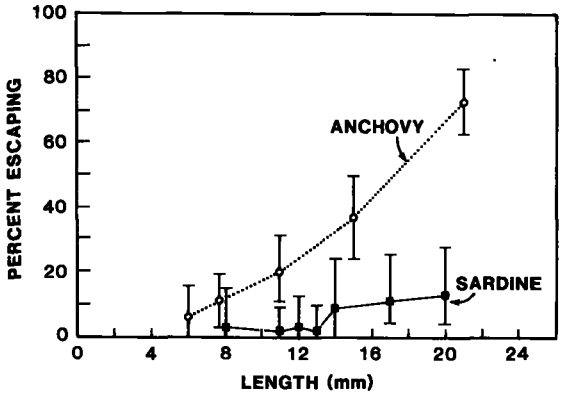

FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

Since the latency of response to attack must be related to the development of the central nervous system (Webb 1981; Webb and Corolla 1981), it may be more appropriate to compare sardine larvae with anchovy larvae of the same age. For that reason lengths of the larvae of both species were converted to age using growth rates measured in the field (Methot and Kramer 1979; Butler 1987). Comparison of the percentage of larvae responding to attack at a given age (Fig. 2) reveals no significant difference in the rate of development of response to attack. Thus, the escape response develops at the same rate in Pacific sardine and northern anchovy, and the difference in proportion of larvae responding at a given size (Fig. 1) is due to the difference of size at hatching and the difference in growth rates of the two species.

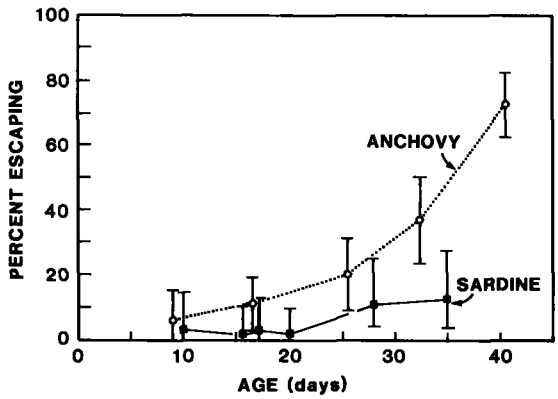

FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

Probability of Escaping Attack

The ability to successfully avoid attack increased with size of Pacific sardine as well as northern anchovy. Few small larvae of either specie escaped attack by adult northern anchovy. Only 3% of 8 mm sardine larvae escaped attack and the percentage of larvae escaping increased to only 11% for 17 mm larvae and 13% for 20 mm

larvae (Fig. 3). The proportion of small anchovy larvae escaping attack was also low (6%) but increased with size to 73% of 22 mm larvae (Folkvord and Hunter 1986). The numbers of larvae escaping attack were significantly different between anchovy and sardines at sizes larger than about 13 mm. Conversion of lengths to age using field growth rates does not eliminate the differences between sardine and anchovy (Fig. 4). Sardine larvae older than 20 days were more vulnerable to predation than anchovy larvae of the same age (Fig. 4).

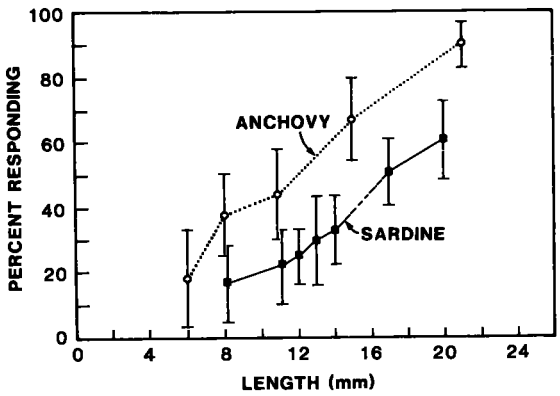

FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

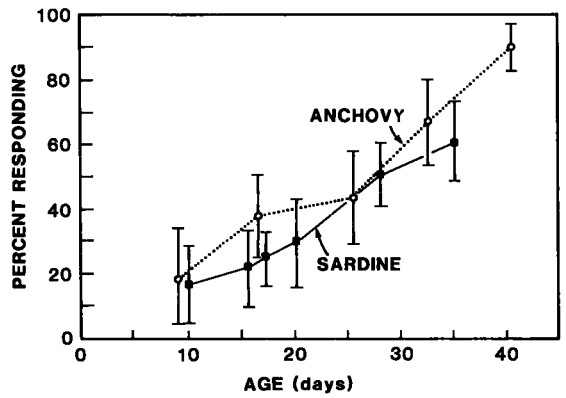

FIGURE 4.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

Discussion

The proportion of Pacific sardine larvae responding to attack and escaping attack increased with size and with age. Our results differ from those reported by Folkvord and Hunter (1986) for anchovy larvae in the rate at which sardine larvae respond and escape attacks at given sizes and ages. It should be noted that, although the methodology was the same, the observers were different. This difference could affect rate of response to attack. It also should be noted that the size of adult anchovy used by Folkvord and Hunter (1986) ranged from 83 to 89 mm SL, whereas the size range was 84–95 mm SL in our study and that the size of predator influences the number of larvae escaping (Folkvord and Hunter 1986). The slightly larger size of predators used in this study is not sufficient to explain difference in escapement, nor is the difference in observer likely to affect the rate of escapement since the observer's task is to examine whether the larvae are escaping or are being eaten.

The greater vulnerability to predation of sardine larvae than anchovy larvae has interesting implications. In general, larger larvae are less vulnerable to predation than small larvae. Bailey (1984) and Bailey and Batty (1983) compared the vulnerability of cod, flounder, plaice, and herring larvae to predation by invertebrate predators. They found that herring larvae were the least vulnerable larvae because herring were more reactive and had the greatest escape speeds. Sardine larvae are larger at hatching and at a given age are larger than anchovy larvae. In our experiment sardine larvae react to predatory attacks at similar rates as anchovy larvae, but escape attack at a much lower rate.

This difference in vulnerability to attack may be due to differences in swimming behavior. Anchovy larvae swim using beat and glide locomotion (Hunter 1972). The escape behavior is usually a burst of swimming from a motionless position (Folkvord and Hunter 1986). We observed that sardine larvae, however, swim continuously and they respond to attack by changing direction and increasing speed. This difference in swimming mode may affect escape behavior in two ways. The escape behavior of sardine larvae may be less flexible than that of anchovy larvae because the direction the sardine larvae takes is largely determined by its trajectory. Since sardine larvae cruise, their scope for activity (escape behavior) may be limited. Anchovy larvae accel-

erate from a standing start and have the possibility of moving in a number of directions. We speculate that the beat and glide behavior of anchovy larvae may not only be hydrodynamically more efficient (Weihs 1974) but also may reduce the vulnerability to predation.

Acknowledgments

Roderick Leong maintained sardines in the laboratory and spawned the adults after manipulation with hormones. Sandor Kaupp reared sardine larvae in the laboratory. Arild Folkvord and Clelia Booman elaborated experimental procedures. John R. Hunter commented on the manuscript.

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INDUCTION OF SPAWNING IN THE WEAKFISH, *CYNOSCION REGALIS*

Reproductive activity in the weakfish, *Cynoscion regalis*, is associated with extensive, north-south migrations that result in spawning in the estuaries of the Middle Atlantic Bight during the late spring and early summer. Spawning is apparently related to increasing water temperature and day length, but there have been no experimental investigations of specific factors that control this process in the weakfish. In contrast, general aspects of the reproductive biology of the species are well known (reviewed by Mercer 1983). Both males and females become sexually mature at 1 year of age, and remain sexually active throughout their lifespan (10^+ years). Spawning involves external fertilization of eggs by pairs or small aggregations of fish.

There has been limited study of larval development in the laboratory, and descriptions of growth and development of larval weakfish come entirely from field investigations (Lippson and Moran 1974). Weakfish larvae resulting from gametes stripped from sexually mature adults captured in the field have been reared for a few days on natural zooplankton diets (Public Service Electric and Gas Company 1984), but no information is available on mortality or growth rates on prescribed diets and rations. In contrast, Houde and Taniguchi (1981) and Taniguchi (1981, 1982) have conducted extensive investigations of the effects of diet, ration, and temperature on growth and survival of larval spotted seatrout, *Cynoscion nebulosus*, under laboratory conditions. Similar studies have been conducted with other sciaenids including red drum, *Sciaenops ocellatus* (Holt and Arnold 1983; Holt et al. 1981), spot, *Leiostomus xanthurus* (Powell and Gordy 1980), and bairdiella, *Bairdiella icistia* (May 1974).

The present paper describes a technique for induction of spawning in a laboratory population of weakfish and provides preliminary information on early development and growth of weakfish larvae.

Methods

Sixteen adult weakfish, *C. regalis*, (approximately 30–45 cm and 0.5–1.5 kg) were captured in September 1984 in Delaware Bay by hook-and-line. Five of these fish were dissected and found to have regressed gonads. The remaining 11 fish were placed in two large tanks (2,000 L) connected to a 20,000 L recirculating system that delivered temperature-controlled seawater to each tank at 10 L/minute. Water in the recirculating system was replaced approximately monthly. Ordinary white room light was provided by two 1.25 m fluorescent lamps positioned 1 m above the surface of the water in each tank. Initial conditions in the tank were similar to ambient conditions in Delaware Bay in September: 18°–19°C, 30‰, and 12 hours light:12 hours dark. Temperature and salinity in the tanks were measured daily and pH approximately weekly. The pH was maintained between 7.0 and 7.6 by additions of new seawater to the system; this was accomplished by replacing 40% of the water in the system with new seawater approximately monthly.

Fish began to feed 5–7 days after capture. Diet consisted of an ad libitum ration of sliced squid with weekly additions of penaeid shrimp or fresh calf liver. After approximately one month in the laboratory, the fish were subjected to a prescribed regimen of temperature and photophase (Fig. 1). Temperatures were lowered and light phase shortened over a period of three weeks until conditions reached 8 hours light, 13°–14°C; this approximated winter conditions on the continental shelf off Cape Hatteras where adult fish are known to overwinter (Merriner 1976). Fish were held under these conditions for 11 weeks after which temperature was gradually raised and light phase increased until spring conditions of 14 hours light and 22°–23°C were reached. Fish were held at these conditions throughout a period of extended spawning activity. After spawning activity ceased, six newly captured fish were placed in the system to replace fish that had died during the previous year, and the process of gradually changing temperature and photoperiod to winter conditions was repeated (Fig. 1).

Fertilized eggs were buoyant and exited the tanks at the surface via stand pipes that emptied into a sump tank. The drain was located at the bottom of the sump tank allowing eggs to accumulate at the water surface. The presence or absence of eggs in the sump was determined daily with a fine-meshed dip net. After collection, eggs from each spawning were allowed to hatch in 20 L plastic aquaria filled with 5.0 μm filtered seawater at 30‰ and 23°C. Eggs exposed to gentle aeration under these conditions hatched in 24–36 hours.

Larvae were cultured in 2 L beakers filled with filtered seawater (25°C, 30‰, and 5 mg/liter

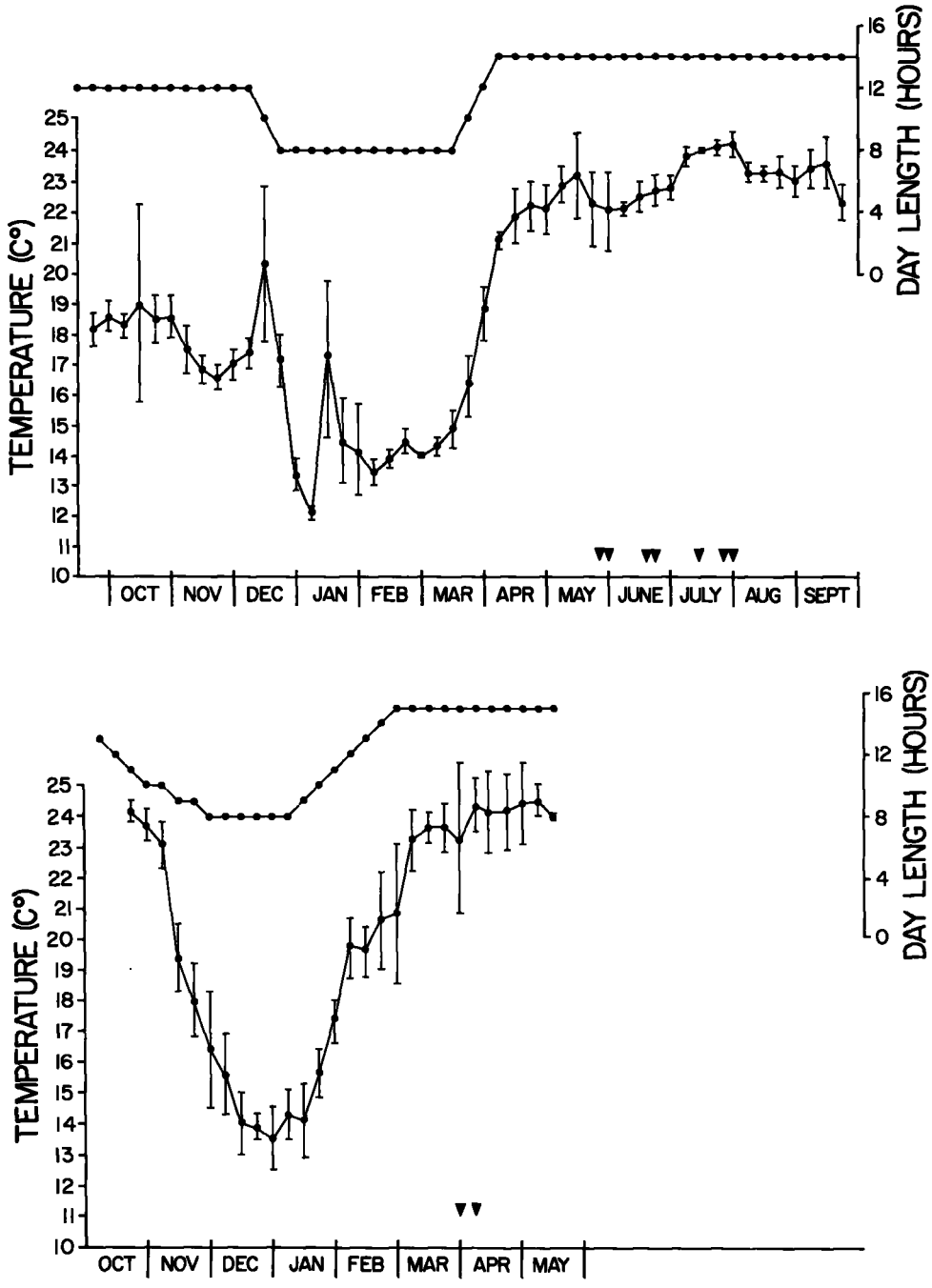

FIGURE 1.—Temperature-photophase regime used to condition northern weakfish, *Cynoscion regalis*, to spawn in the laboratory. Values are 7-d means. Standard deviations are plotted for temperature. Arrows on time axis indicate dates of spawning. A = 1984–85. B = 1985–1986.

chloramphenicol) at a density of 25 larvae/liter. Larvae were fed rotifers, *Brachionis plicatilis*, beginning two days after hatching; on the seventh day after hatching, brine shrimp *Artemia* sp. were added to the diet.

Early larval development from spawning to first feeding was determined for larvae from three separate spawnings. Newly hatched larvae (6–15 hours old) were pipetted into an aquarium and 10–15 removed immediately and preserved in 70% ethanol. Additional larvae were sacrificed daily for nine days. These samples were examined to relate early development and age.

Results and Discussion

Three adult fish died of undermined causes during the period of winter conditions in 1984–85. Four additional fish died after jumping from the tanks. The initial spawning by the remaining population of four fish occurred five weeks after spring conditions were achieved. This was followed the next day by another spawning. Spawning continued for nine weeks at 10–14 d intervals. Spawning episodes usually consisted of production of fertilized eggs over 2 successive days. While actual spawning was never observed, it always occurred between sunset and 08:00 the following day.

After cessation of spawning, the four fish were removed from the tanks and their sex determined. Two of the fish drummed when handled and were clearly males. At least one (and probably both) of the two remaining fish were females. The fish were returned to the system after examination.

The temporal sequence of the spawning events (two successive days at 10–14 d intervals) suggests that each female may have spawned as many as four times during the 9-wk period. This is in contrast to reports for natural populations of *C. regalis* (e.g., Merriner 1976), but has been reported for laboratory populations of other sciaenid fishes. For example, Arnold (1984) observed 82 spawning events in a laboratory population of 12 *C. nebulosus* over a 27-mo period and 52 spawning events in a similar population of six *S. ocellatus* over a 3-mo period. It is not clear why the *C. regalis* in our investigation ceased spawning after several months of long days and high temperatures while the *C. nebulosus* in Arnold's system continued to spawn over a much longer period. Perhaps this is related to the smaller annual variation in photophase and temperature typical of *C. nebulosus* habitats. However, gonadal resorption has been reported for at least one other sciaenid species (*B. icistia*) held in the laboratory for extended periods of long day-length (May 1974).

Spawning from the 1985–86 conditioning period first occurred four weeks after spring conditions were reached with a second spawning nine days later. Further spawning in the 1985–86 population did not occur because of an unidentified infection resulting in the death of all 10 fish in the system over a period of a few weeks. Autopsies revealed that all fish had highly developed ovaries or testes at the time of death.

Newly hatched larvae (6–15 hours old) had a yolk sac, no mouth, and little development of the eyes. By 24–36 hours after hatching, the yolk sac had been virtually absorbed, the mouth was just beginning to form, and the eyes were not yet pigmented. By 48–60 hours, larvae had a completely formed mouth and digestive system, and the eyes were pigmented. Larvae were capable of feeding at this stage.

Chloramphenicol improved larval survival, which was as high as 24% over 11 days. This survival is comparable to that reported for other sciaenid larvae (Holt et al. 1981; Houde and Taniguchi 1981; Holt and Arnold 1983). However, growth was less than the maximum seen in the laboratory for *C. nebulosus*. After 11 days *C. regalis* larvae in the present experiments had grown from a mean, posthatching size of 2.7 mm (36 μg dry weight) to 4.5 mm (235 μg dry weight). In contrast Houde and Taniguchi (1981) found that one group of *C. nebulosus* larvae reached a size of 13.6 mm (7,082 μg dry weight) in 12 days when reared on a concentrated ration of natural zooplankton at very low stocking density and high temperature (32°C). However, when fed a rotifer diet at comparable temperatures and stocking densities, growth of *C. nebulosus* larvae was somewhat less than that of *C. regalis* larvae in the present experiments.

Our results show that the spawning cycle of weakfish can be manipulated to produce repeated spawnings without the aid of hormone injections. While the fish appear to resorb their gonadal tissue after several months of exposure to long day length and high temperature, the differential manipulation of several groups of fish could allow year-round production of fertilized eggs. Furthermore, survival and growth of larvae produced in this manner appear comparable to survival and

growth of other sciaenids reared in the laboratory.

Acknowledgments

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ERRATA

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Botton, Mark L., and John W. Ropes, "Populations of horseshoe crabs, *Limulus polyphemus*, on the northwestern Atlantic continental shelf," p. 809.

Page 809, Table 3, footnote was omitted:

[1]Depth at the end of this tow was 439 m.

Henwood, Tyrrell A., and Warren E. Stuntz, "Analysis of sea turtle captures and mortalities during commercial shrimp trawling," p. 814.

Page 814, paragraph 1, line 3, the equation should read:

$$E = (\text{nets} * \text{length}/30.5\ \text{m}) * (\text{min}/60)$$

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MIGRATIONS OF COHO SALMON, *ONCORHYNCHUS KISUTCH*, DURING THEIR FIRST SUMMER IN THE OCEAN

WILLIAM G. PEARCY AND JOSEPH P. FISHER[1]

ABSTRACT

Marked juvenile coho salmon caught in fine-meshed purse seines during the summers of 1981–84 off Oregon and Washington generally demonstrated northward migrations from their rivers of ocean entrance. Northward movements in summer were preceded by southerly movements during spring, probably caused by southerly advection. Catch rates and sizes of fish caught in different months and regions of the coast also indicated northerly movements of both yearling and subyearling coho salmon. Despite this movement, the average catch of juvenile coho salmon per purse seine set along the coasts of Washington and Oregon in late summer, including marked fish from the Columbia River, was still a substantial proportion of that in May and June soon after ocean entrance, suggesting that many coho did not migrate great distances. Additionally, recoveries of marked juvenile coho salmon by sports and commercial fishermen from Alaska to California and by scientists in Alaska were generally in the region of release. These data indicate that migrations of juvenile coho are of limited extent during their first summer in the ocean and are not strong support for an earlier conclusion that juvenile coho salmon from the Columbia River, Oregon, and California may form a large proportion of the stocks of this species that migrate northward along the coastal belt in Canadian and Alaskan waters each summer.

Although there has been little research on juvenile salmon during their first summer at sea, this phase of the life history may be critical to survival and recruitment to fisheries (Hartt 1980). Highest ocean mortality is thought to occur early in marine life (Foerster 1968; Parker 1968; Ricker 1976). Production (catch and escapement) of adult coho salmon, *Oncorhynchus kisutch*, in the Oregon Production Index (OPI) Area (from Leadbetter Point, WA, to Monterey Bay, CA) is usually accurately predicted in one year by the number of precocious males (jacks) returning to index streams in the previous year (Gunsolus 1978; Oregon Department of Fish and Wildlife 1982; Pacific Fishery Management Council 1986). Hence survival from jacks to adults is fairly constant from year to year. Because survival rates from smolt to adult are variable (Nickelson 1986), however, variable year-class survival must occur before the time that jacks return, after only a few months in the ocean. This relationship, and the positive correlation between coastal upwelling and survival of OPI coho salmon (Gunsolus 1978; Scarnecchia 1981; Nickelson 1986), strongly suggest that the first few months in the ocean constitute the "critical period" in determining subsequent adult survival.

Between 1976 and 1985 the production of coho salmon in the OPI area drastically declined, despite large increases in the number of public and private smolt releases (Oregon Department of Fish and Wildlife 1982; Nickelson 1986). Reduced upwelling and ocean productivity, perhaps coupled with density-dependent mortality, is one of the hypothesized causes for this decrease in survival (Scarnecchia 1981; Peterman and Routledge 1981; McCarl and Rettig 1983; McGie 1984; Nickelson 1986). To understand the mechanisms affecting survival of juvenile salmonids at sea, we must first know where salmon reside at the time of their high and variable mortality. Are the smolts highly migratory, immediately leaving local coastal waters and migrating into waters of the Gulf of Alaska (Hartt and Dell 1986), or are they nonmigratory, spending their early ocean life in local coastal waters?

This paper summarizes research on the movements and migrations of coho salmon during their first summer in the ocean in the northeastern Pacific Ocean based on purse seine catches made mainly in coastal waters off Oregon and Washington. A few records of migrations of tagged juvenile (age .0)[2] coho salmon were given by God-

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[2]The numeral preceding and following the decimal indicate the number of winters spent in fresh water and in the ocean, respectively.

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frey (1965) and French et al. (1975), but by far the most comprehensive data were provided by Hartt (1980) and Hartt and Dell (1986). All of these studies, however, were based on recovery of mature or maturing coho in the year following tagging and on tagging in northern waters from the Strait of Juan de Fuca to the Alaska Peninsula. The only other studies of juvenile salmon in the ocean off Washington and Oregon have been restricted to within 24 km of the Columbia River (Dawley et al. 1981) or to coastal waters during 1980 (Miller et al. 1983). Our 1979–85 research, covering large areas along the coast, provides extensive and unique data on the movements of juvenile coho salmon during their first summer in the ocean.

METHODS

Purse seines, our primary sampling method, were used to sample juvenile salmonids during 1979–85 (Table 1). Cruises were in coastal waters off Oregon in 1979–80, off Oregon and southern Washington in 1981, and off Oregon and the entire Washington coast during the summers of 1982–85 (Fig. 1). During July 1984, sets were also made from northern California (lat. 40°32'N) to northern Vancouver Island (50°26'N). Except for the exploratory cruises off Oregon in 1979 and 1980, purse seine sets were usually made along east-west transect lines (Fig. 1). Sets started at the 37 m (20-fathom) contour, and continued at 9.3 km (5-mi) intervals farther offshore, usually until no salmonids were captured. Repeat sets were sometimes made when fish with missing adipose fins were common, indicating the presence of coded wire tagged (CWT) fish. In 1985, special sets were made in the vicinity of the Columbia River plume. Detailed sampling data are provided in Pearcy (1984) and our cruise reports (Wakefield et al. 1981; Fisher et al. 1982, 1983; Fisher and Pearcy 1984, 1985).

The mesh size of the seines were the same during all years, 32 mm (stretch), with 32 mm or smaller mesh in the bunts of the seines. The seine was 495 m long except in 1981 (457 m). Depths that seines fished, sometimes measured with a depth gauge on the lead line, varied among years from about 20 m to 65 m (Table 1).

Generally, purse seine sets were "round hauls", where the seiner and the skiff made a circle with the net. The seine was fully pursed after about one-half its length was aboard (half-purse sets). All sets were "blind". We attempted to use sonar on some cruises to locate concentrations of salmonids but were unsuccessful. Radar was sometimes used to determine the distance between the seiner and the skiff when a semicircle was made with the net. Each round haul encompassed about 17,000 m^2 (1981) or 19,000 m^2 (1979–85). To determine the direction of movement of fish, eight "half-round" hauls, or "semicircular" sets, were made in 1979, where the entire net formed an open semicircle. Paired sets were made in close succession, with sets open in a northern and a southern direction, at four locations. The seine was open for the same duration (15–45 minutes, depending on location) in each paired set while

TABLE 1.—Summary of number of purse seine sets and latitudinal range of sampling, 1979–85.

Year	Dates of cruises	No. of sets[1]	Latitudinal range of sampling		Purse seine Length (m)	Purse seine Depth (m)
1979	18–29 June	56	Cape Disappointment to Cape Arago	46°20'–43°18'	495	20
1980	20–28 June	36	Cape Disappointment to Alsea River	46°20'–44°30'	495	20
1981	16–25 May	63	Willapa Bay to Alsea River	46°35'–44°25'	495	20
	9–18 June	67	Willapa Bay to Cut Creek	46°35'–43°11'	495	20
	9–19 July	67	Willapa Bay to Alsea River	46°35'–44°25'	457	49
	8–19 Aug.	66	Willapa Bay to Cut Creek	46°36'–44°11'	457	49
1982	19 May–2 June	62	Waatch Point to Siuslaw River	48°21'–44°00'	495	265
	7–22 June	57	Quinault River to Yachats	47°21'–44°20'	495	265
	4–14 Sept.	42	Quinault River to Yachats	47°20'–44°19'	495	265
1983	16–27 May	56	Waatch Point to Yachats	48°21'–44°20'	495	249
	9–27 June	58	Waatch Point to Four Mile Creek	48°20'–43°00'	495	249
	15–24 Sept.	53	Waatch Point to Coos Bay	48°20'–43°28'	495	249
1984	4–20 June	69	Waatch Point to Coos Bay	48°20'–43°27'	495	249
	9 July–3 Aug.	65	Winter Harbor, B.C. to False Cape, CA	50°26'–40°32'	495	249
	1–15 Sept.	63	Waatch Point to Siuslaw River	48°20'–44°00'	495	249
1985	29 May–25 June	112	Sea Lion Rock to Coos Bay	48°00'–43°27'	495	225

[1]Quantitative sets.
[2]Measured with depth guage.

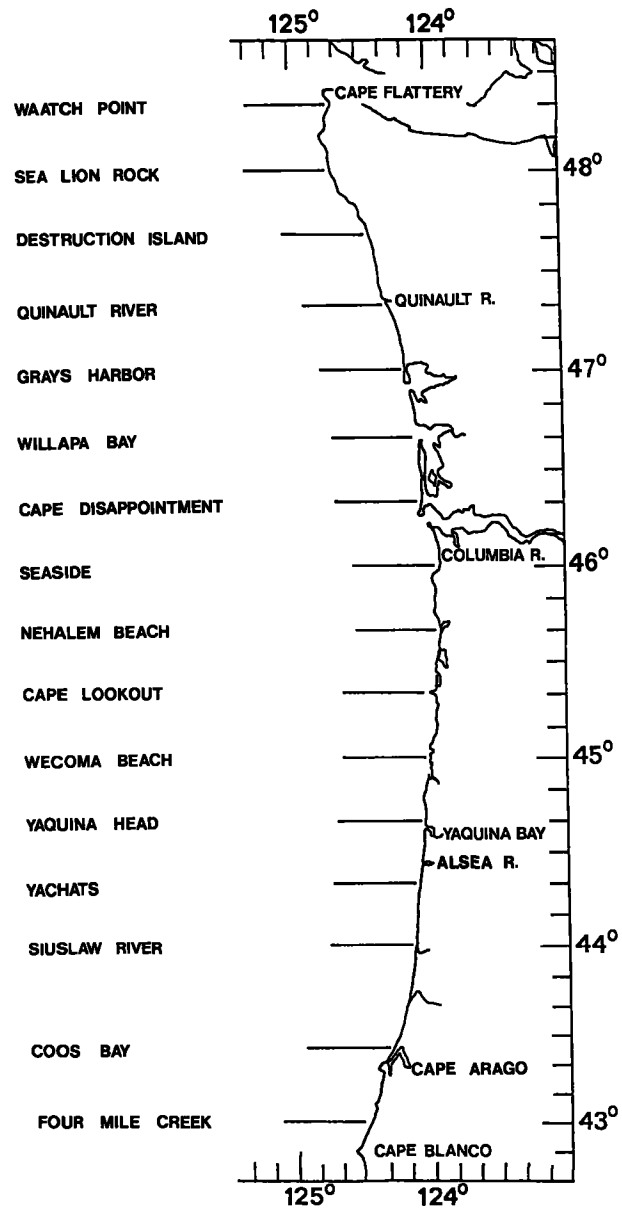

FIGURE 1.—Locations of purse seine transects off the Oregon and Washington coasts.

the vessel and skiff towed the seine only fast enough to maintain a constant net opening.

The purse seine catches were either dip-netted from the bunt of the seine while it was alongside the vessel, brailed aboard, or hauled aboard in the bunt, depending on the composition and size of the catch.

In 1979 and 1980, juvenile salmon preserved in formalin were identified ashore. In 1981–85, juvenile salmon were identified to species at sea, fork length (FL) was measured to the nearest millimeter and then they were individually wrapped in labelled plastic bags and frozen. All salmonids with marks or missing adipose fins were frozen. When large numbers of juvenile salmonids were caught in a set, most unmarked fish were released after they were measured.

In order to increase the numbers of marked fish released into our study area we marked about 1.5 million coho smolts in 1981 and 835,000 in 1982 using fluorescent pigment propelled by compressed air (see Phinney et al. 1967) prior to their

transport from Oregon Aqua-Foods, Inc. (OAF) hatchery to their ocean release facilities at Yaquina Bay or Coos Bay, OR.

In the laboratory ashore, species identifications were confirmed and individuals remeasured and reexamined for both fluorescent marks (under ultraviolet light 1981–82) and missing adipose fins or other marks (1979–85). Coded-wire tags from the heads of salmonids with missing adipose fins were decoded by personnel from the Oregon Department of Fish and Wildlife, Clackamas Laboratory.

Juvenile or age .0 (first year in the ocean) coho salmon were distinguished from adult or age .1 (second year in the ocean) coho salmon by examination of size-frequency histograms and scales. The division between age .0 and .1 coho progressed from approximately 300 to 420 mm FL from May to September, in most years. Most coho salmon migrated to the ocean a little over one year after hatching (age 1.0), but OAF released large numbers of subyearling (age 0.0) smolts into Yaquina Bay and Coos Bay. These two age groups of smolts were distinguished by the radial distance to the 21st circulus on scales removed from the preferred area (Clutter and Whitesel 1956) of the fish. The accuracy of this method for distinguishing known age 0.0 and 1.0 fish was approximately 85–90%. In the years 1981–85, scales from 52% of the 4,222 juvenile coho sampled were analyzed. The estimated numbers of age 0.0 and 1.0 fish represented in different geographic areas and cruises were then extrapolated from their proportions in each 10 mm length interval.

Distances traveled and movement rates were estimated from actual distances between sites of release and entry into the ocean, and from straight-line distances between ocean entry and recapture locations for CWT or fluorescent marked juvenile coho salmon that were recovered in the ocean within 10 days of release. These distances and swimming speeds are minimal estimates.

In addition to purse seining, fine-meshed monofilament gill nets were used off the Oregon coast (ca. lat. 45°00'N, long. 124°21'W) during 24 and 25 July 1985, from the training vessel *Oshoro Maru*, to determine depth and direction of swimming of juvenile salmonids. Surface and subsurface nets were used. The surface gill nets were 2,050 m long, and fished from depths of 0–6 m with 11 mesh sizes ranging from 29 to 121 mm (stretch). The subsurface nets were 500 m long and consisted of four mesh sizes ranging from 29 to 42 mm; they were suspended below large (300–400 mm) mesh to fish at depths of 5–12 m. Four sets were made in an east-west direction with soak-times of about 4–9 hours. As the gill nets were hauled, the direction that each juvenile salmonid was heading when caught, and its depth in the net (upper, middle, or lower section) were noted. Each juvenile salmonid was given a consecutive number and frozen for later identification. Comparisons of catch rates in the surface and subsurface nets were based on equal lengths of the four mesh sizes of the subsurface net, standardized to 10 hours of fishing time.

Information on the location of landings of marked juvenile coho by commercial and sports fishermen was provided by the Pacific Marine Fisheries Commission (PMFC), (PMFC 1980, 1981, 1984a, b, c, 1985a, b), from lists of nonstandard recoveries (Johnson PMFC unpubl. data), and from state agencies. The actual numbers of tagged fish, and the total numbers of tagged fish estimated from the proportions of the catch sampled are reported.

To determine if juvenile coho salmon were sexually precocious "jacks", we examined testes from 542 juvenile males caught in July 1981 and 1984, in August 1981, and in September 1982, 1983, and 1984. All developed and some undeveloped testes (ribbonlike, with no thickening), as determined by visual inspection, were weighed (123) and gonadal-somatic indices (GSI = testes wt./body wt. × 100) were determined.

RESULTS AND DISCUSSION

Swimming Direction

Of the 106 juvenile coho salmon captured during June in paired, half-round purse seine sets, all but two were in the sets open to the south (Table 2). This suggests that juvenile coho salmon

TABLE 2.—Catches of coho salmon in semicircular purse seine sets open to the south (S) and north (N) off Oregon, June 1979.

		Age .0		Age .1	
Location	Km offshore	S	N	S	N
Clatsop Spit	12.6	57	0	2	6
Clatsop Spit	18.5	37	0	15	37
Clatsop Spit	18.5	7	0	6	8
Newport	9.4	3	2	0	9
		98%	2%	28%	72%

were swimming to the north during this sampling period. Maturing fish over 300 mm FL (age .1 coho) showed the opposite trend.

Miller et al. (1983) made several hundred paired purse seine sets open to the south and north during three cruises off the northern Oregon-southern Washington coasts in 1980. During their May-June cruise, they caught 76% of the juvenile coho salmon, 80% of the chinook salmon, and almost all the steelhead trout in sets open to the south, indicating northward movement. We note a positive relation between the proportion of juvenile salmon caught in south-facing sets in their three cruises and strength of upwelling during these cruises (mean daily Bakun indices of 52, 39, and 19 $m^3 s^{-1}$ 100 m^{-1} coastline at 45°N, 125°W in May, July, and August, respectively (Mason and Bakun 1986)), suggesting that surface currents to the south resulting from Ekman transport may be cues for orientation of salmon smolts.

Hartt (1980) and Hartt and Dell (1986) found that 83% of the combined species of juvenile salmonids caught in 19 paired purse sets along the coast from Cape Flattery, WA to Yakutat, AK were caught in sets held open to the southeast and only 17% in sets open to the northwest and north. They concluded that juvenile salmonids tended to migrate in a northwest direction along the coast during July–September.

Of the 100 juvenile coho salmon (135–315 mm FL) caught in the gill nets set in an east-west direction off the Oregon coast in July 1985, 90 coho were caught as they approached the southern face of the gill net (heading north) and 10 in the northern face (heading south). Jaenicke et al. (1984) reported that 63% of the juvenile coho caught in a surface gill net fished off southeastern Alaska in July moved north at night, but only 6% moved to the north during the day.

Available data indicate that most juvenile coho salmon caught off Oregon and southern Washington, as well as juveniles farther to the north, are predominantely swimming in a northerly direction during summer months.

Depth Distribution

One-half of the juvenile coho salmon caught in gill nets set off the Oregon Coast in 1985 were in the upper 2 m of the surface gill net (Table 3). Catches in the surface net exceeded those in the subsurface net, except for the last set that fished during daylight hours, indicating that juvenile coho salmon were most common in the upper 4 m of the water column.

Other information on the vertical distribution of maturing coho and other species of salmon caught in gill nets or with longlines in oceanic waters also indicates that they usually swim near the surface, between 0 and 20 m (Manzer 1964; Godfrey 1965; Godfrey et al. 1975). Machidori (1966), for example, fished gill nets from the surface to 50 m and caught 79% of the coho salmon in the upper 10 m of the gill net. Although catches in gill nets at different depths may be biased by vertical differences in avoidance reactions to the net or swimming speeds (Hartt 1975), acoustical methods have also shown that salmon are usually distributed near the surface (Susuki and Sonoda 1972; Lord et al. 1976). We conclude that most juvenile coho salmon in coastal waters and maturing coho in oceanic waters reside at depths above 20 m, the minimum depth that our purse seine fished. We recognize, however, that maturing coho and other species of salmon may feed in deeper water. Some salmon (including coho salmon) caught in surface gill nets in the oceanic waters of the Gulf of Alaska contained prey in their stomachs characteristic of mesopelagic depths (200–1,000 m), suggesting that some individuals may feed well below the thermocline (Pearcy et al. in press).

TABLE 3.—Catches of juvenile coho salmon in four gill net sets in 50 m lengths of 29, 33, 37, and 42 mm mesh at different depths and times 24–25 July 1985, each set adjusted to 10-h fishing duration.

	Depth in meters					
	Surface net			Subsurface net		
Times of set	0–2	2–4	4–6	5–7	7–9	9–12
0913–1702	2.5	3.8	0	1.3	1.3	0
2001–0104	25.0	11.5	0	0	0	1.9
0248–0701	42.8	2.4	2.4	9.5	16.6	0
0830–1737	1.1	0	0	6.6	7.7	5.5
Total catch	51	16	1	11	15	6
Percent of total catch	50.3	12.5	1.7	12.3	18.0	5.2

North-South Trends in Catch per Set and Sizes of Juvenile Coho

Variations in the average catches and sizes of juvenile coho salmon in purse seine sets in different regions of the Oregon-Washington coast during the summer provide indirect evidence for north-south coastal movements. Histograms showing average catches per set for 10 mm size

groups of juvenile coho, classified as age 0.0 or 1.0 from scale analysis, are shown in Figure 2, for 1981–84 in three regions: (A) Cape Flattery, WA to Grays Harbor, WA (called Washington), (B) Willapa Bay, WA to Nehalem Bay, OR (Columbia River region), and (C) Cape Lookout, OR to Coos Bay, OR (Oregon) (Fig. 1). In May of 1981, 1982, and 1983, average catch per set of yearling (age 1.0) coho generally decreased from the southern to the northern regions. Catches were highest off Oregon (Area C) or the Columbia River (Area B) and lowest off Washington (Area A) in May of 1982 and 1983. This trend was reversed later in the summer. In June of 1981, 1983, and 1984, lowest catches were found in the Oregon region. By August or September 1981–84, highest catches consistently occurred off the Columbia River or Washington and few yearling fish were caught off Oregon. These shifts in abundance suggest a northerly movement of age 1.0 smolts during the summer. Highest catch rates occurred in May and June of 1981 and 1982 when an average of over 10 juvenile coho salmon were caught in most sets.

Subyearling or age 0.0 coho salmon released from private facilities at Yaquina and Coos Bays provide more direct evidence on movements. Subyearling coho salmon clearly demonstrated northward dispersal. They were most common in our catches of July 1981 and September 1982, 1983, and 1984 (Fig. 2). They were apparently more numerous than age 1.0 coho salmon in the Oregon region during June–August 1981 and September 1982, and in the Oregon and Columbia River regions in September 1983. The catches and proportions of age 0.0 coho salmon increased off Oregon during the summer because they were released from hatcheries later in the summer than yearling coho salmon. They were found in the most northern region sampled late in the

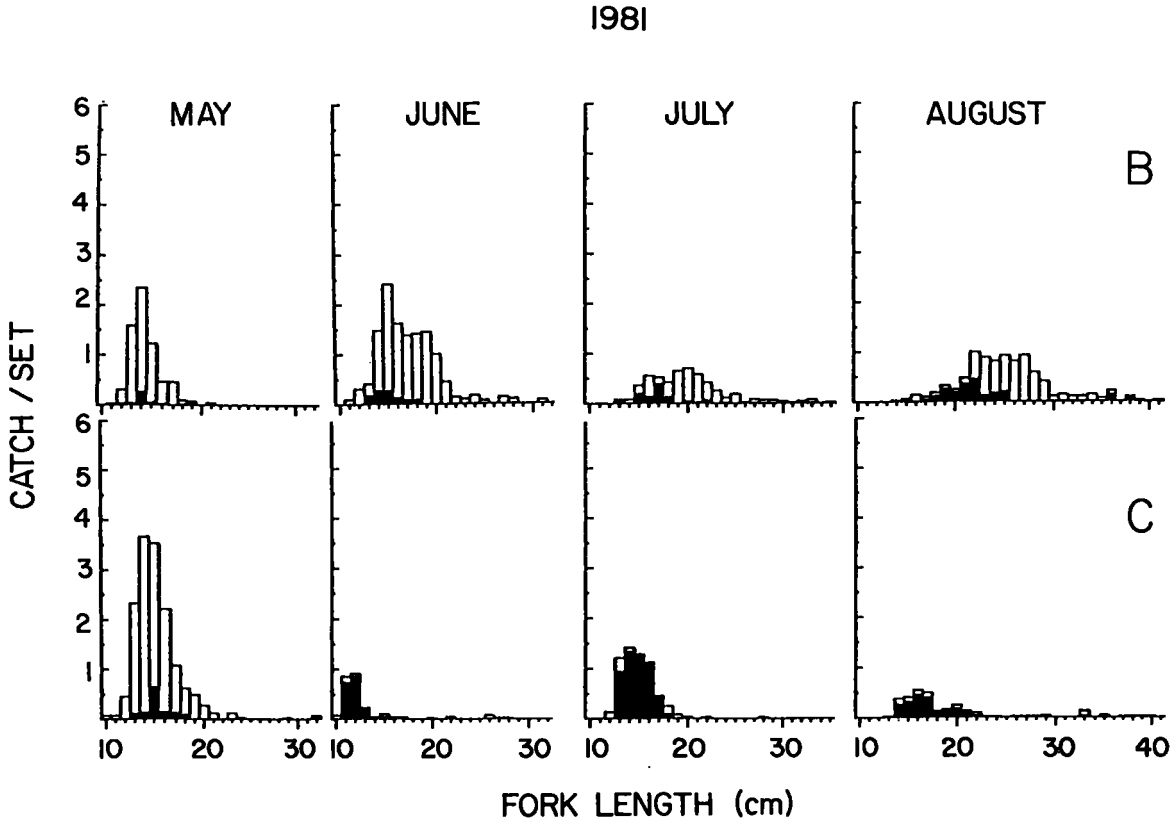

FIGURE 2.—Catch per purse seine set of age 1.0 (open) and age 0.0 (shaded) juvenile coho by 10 mm length groups during different months, 1981–84, for three regions of the Oregon-Washington coast: (A) Cape Flattery to Grays Harbor, WA, (B) Willapa Bay, WA to Nehalem Beach, OR, (C) Cape Lookout to California.

summer of all years. Their abundance, as that of age 1.0 coho salmon, also increased during the summer off Washington where they intermingled with age 1.0 coho salmon. Because the Oregon region included the release locations of all age 0.0 coho salmon, our figures provide no information on southward movements of these fish.

The mean lengths of both age 0.0 and 1.0 coho salmon increased from the southern to the northern areas during most months. Larger age 0.0 and 1.0 coho salmon were caught off Washington than Oregon during the late summer, 1981–84 (Fig. 2), providing corroborative evidence for northward migration of coho salmon. Larger, and presumably older, fish were found farther to the north than smaller fish.

Despite northward movements, many yearling coho salmon did not migrate out of the sampling area, but remained in coastal waters off Oregon and Washington during the entire summer. Mean coastwide catch per set of yearling coho salmon in August 1981 and September 1982, 1983, and 1984

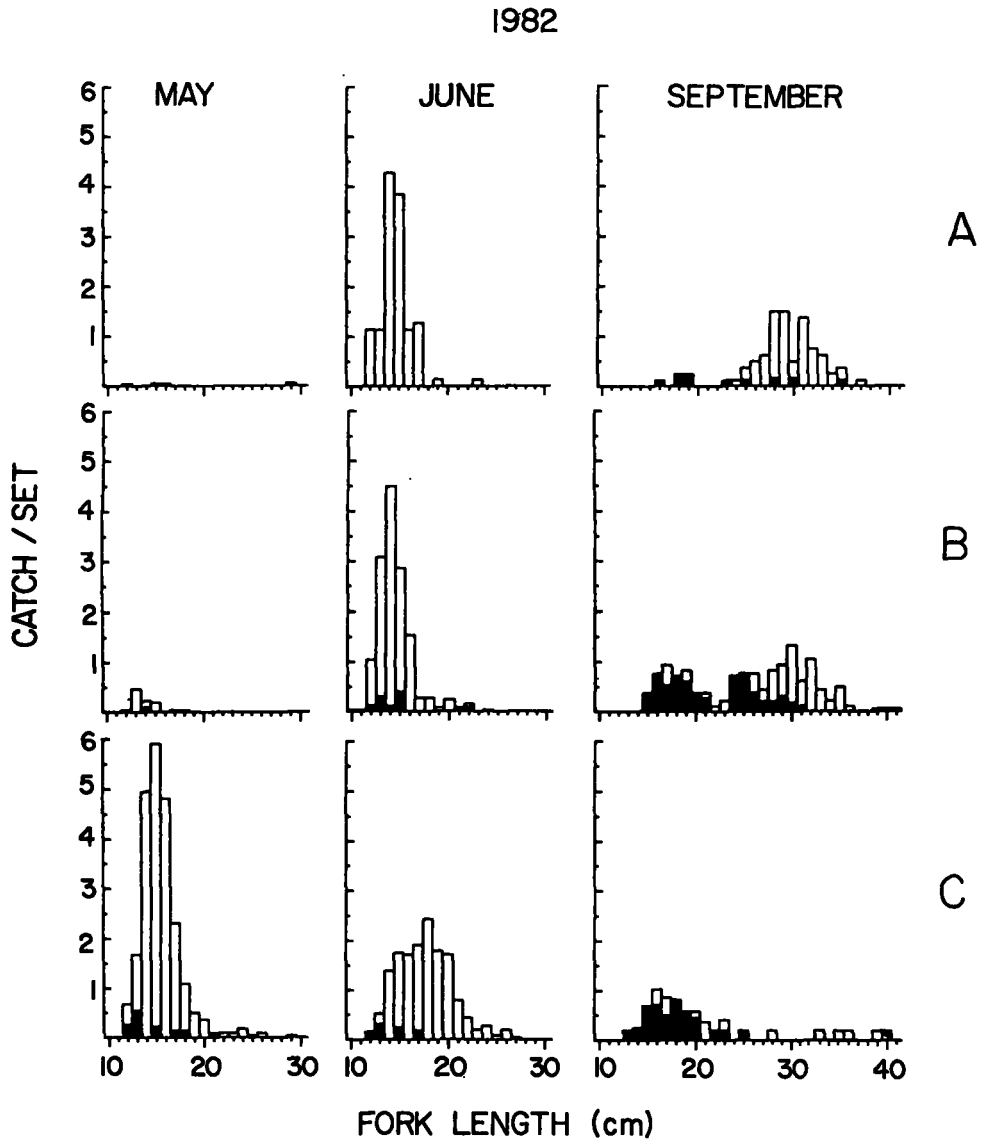

FIGURE 2.—*Continued*.

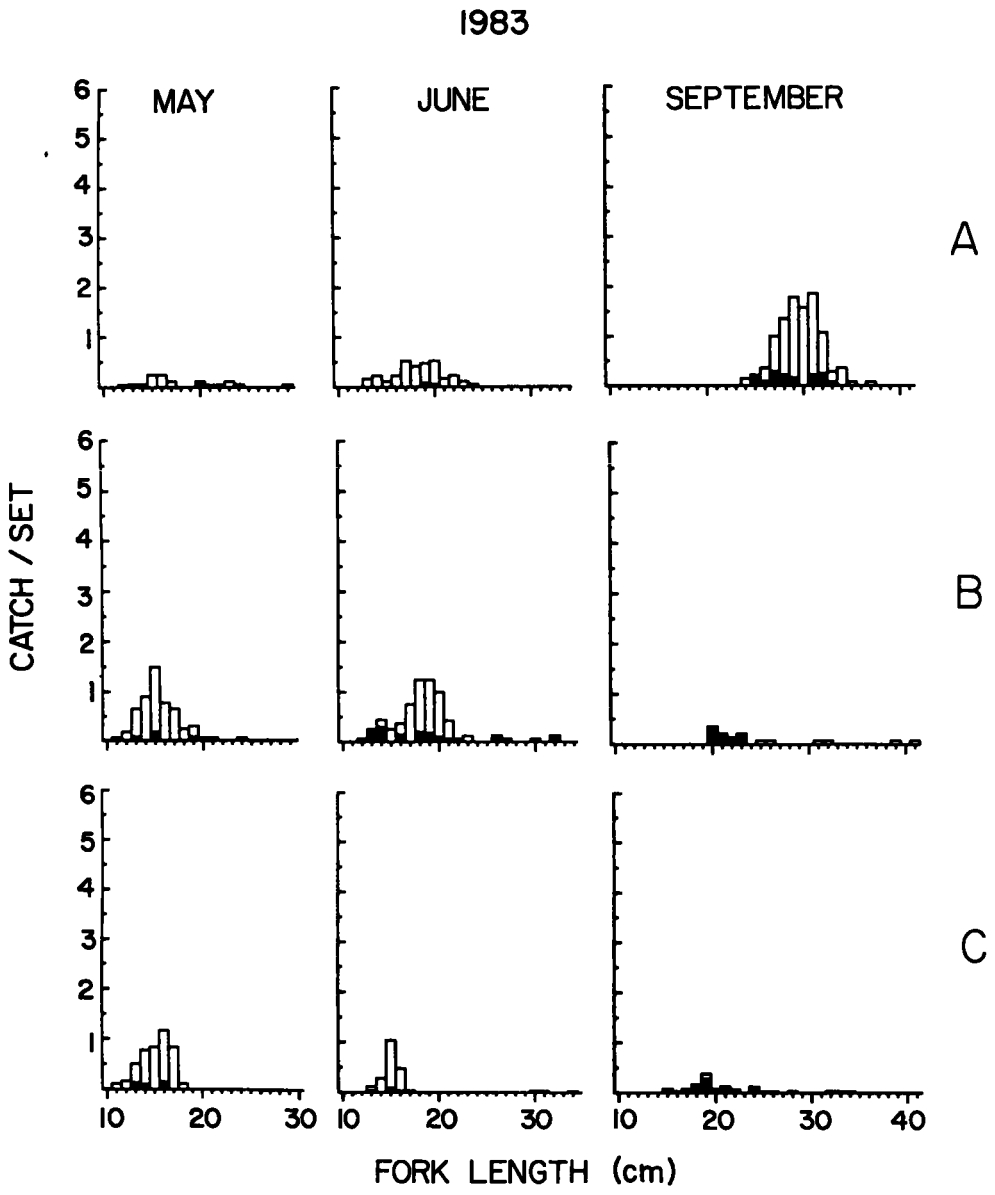

FIGURE 2.—*Continued*.

was 61%, 42%, 81%, and 77% respectively, of that in June of the same years. In September 1983, a strong El Niño year (Pearcy and Schoener 1987), almost all yearling juvenile coho salmon were caught at the extreme northern transect off Cape Flattery, but in August or September of other years they were more evenly distributed off the Columbia River and the Washington coast.

In July 1984, we sampled both north (15 sets off the west coast of Vancouver Island) and south (5 sets off northern California) of Washington and Oregon. Catches per set of yearling and subyearling juvenile coho salmon were higher off the Columbia River (5.1), the area of greatest smolt production, and off Washington (3.5) than off Vancouver Island (1.8), Oregon (1.7), and California (1.2). This shows that as late as July juvenile coho salmon occurred in coastal waters of all regions and were not concentrated off Vancouver Island or California.

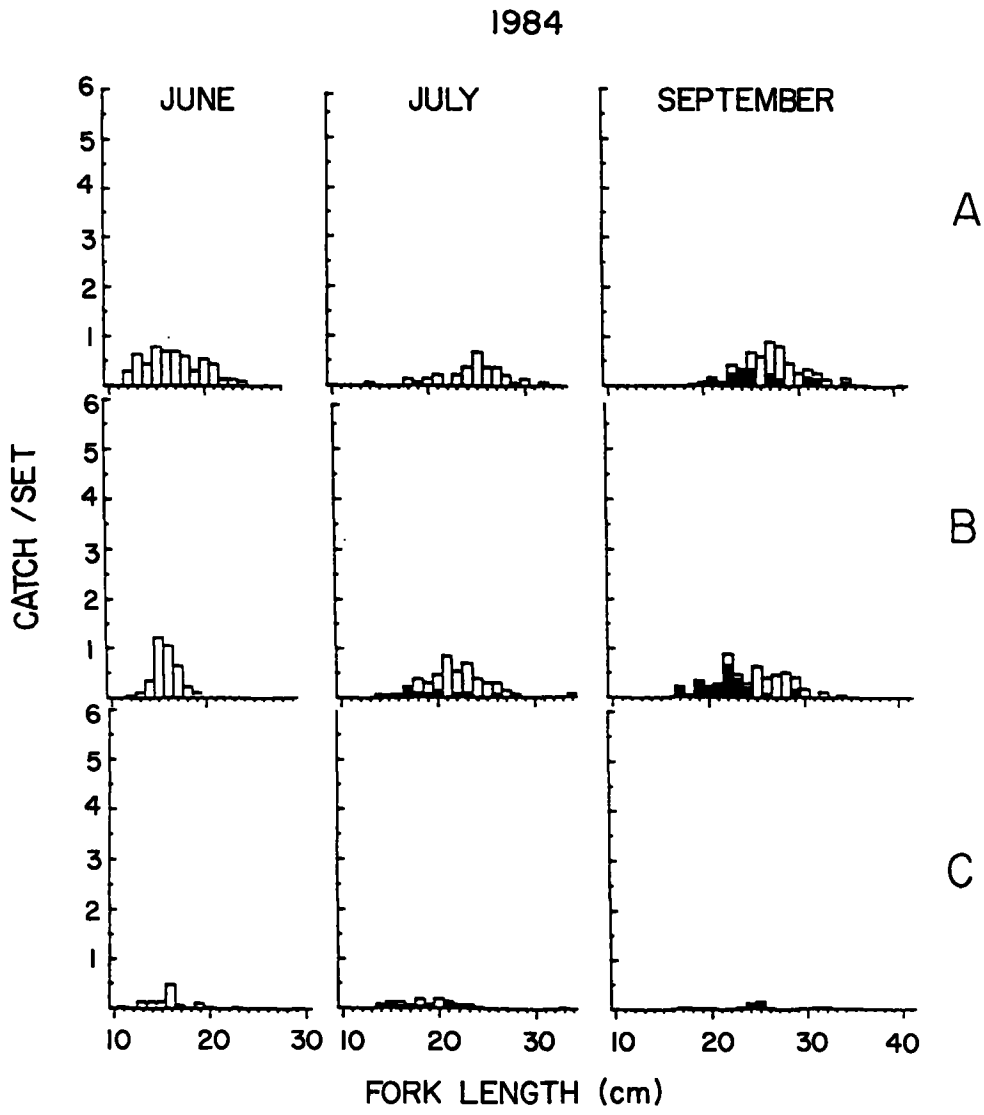

FIGURE 2.—*Continued*.

The Question of "Jacks"

Are the juvenile coho salmon off Oregon and Washington in late summer relatively nonmigratory because they are sexually precocious? GSI were almost always <0.1% for those fish visually classified as "undeveloped". GSI's from fish with "developed" testes ranged from 0.2% to 1.0% in July 1981 and 1984 in fish >250 mm FL; from 0.3% to 5.6% in August 1981, mostly in fish >280 mm FL; and from 2.4% to 6.6% (except for one value at 0.6) in September 1982, 1983, and 1984 in fish >300 mm FL (Fig. 3). In August 1981, and clearly in September 1982, 1983, and 1984, two distinct groups of fish were evident: "jacks", with developing testes (GSI >0.3% August or GSI >2.0% September), and "nonjacks", which showed no development (GSI <0.1%).

The total numbers of jacks and nonjacks in each 50 mm length group were estimated for the catch during August 1981 and September 1982, 1983, and 1984 from the ratio of jacks and nonjacks in the sample (Table 4). Only 8.4%, 4.8%, 5.2%, and 2.8% of all juvenile fish (male and female) were "jacks" in August 1981 and September 1982, 1983, and 1984, respectively. However jacks com-

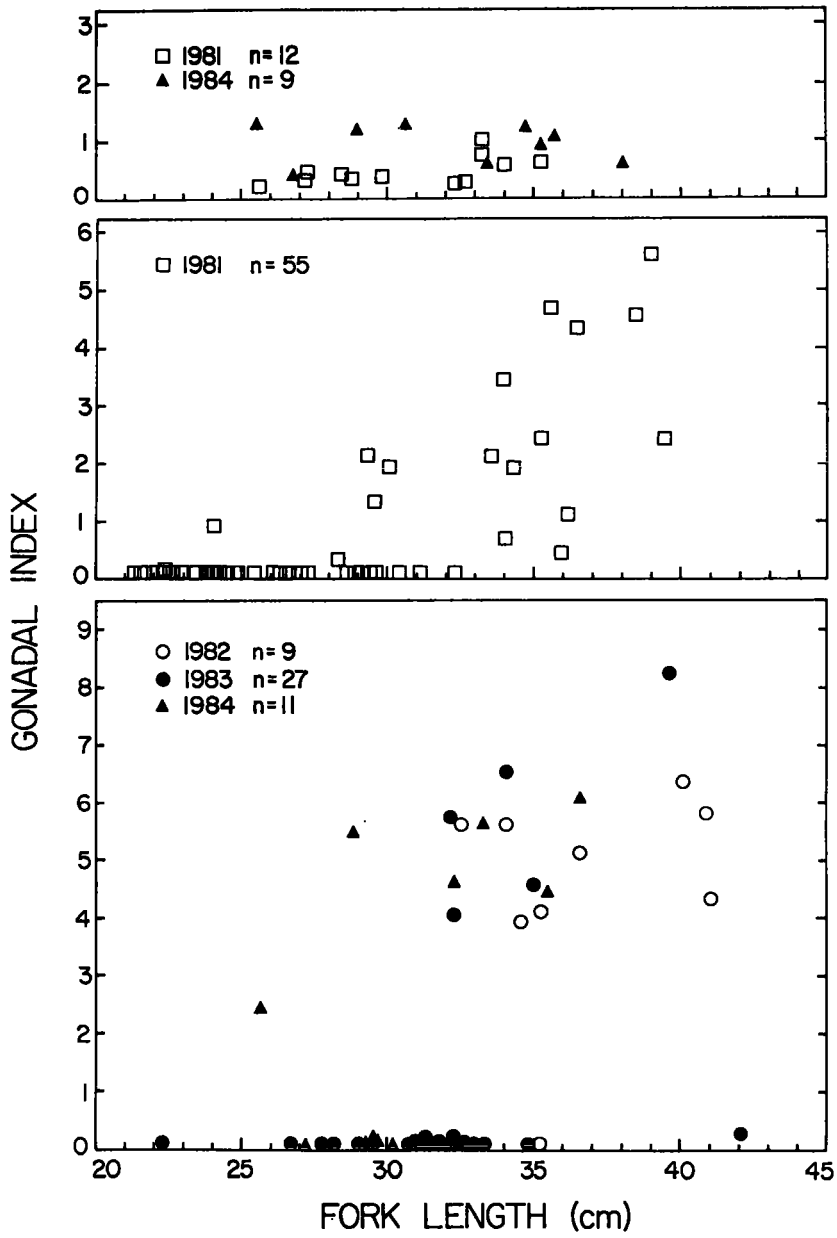

FIGURE 3.—Gonadal-somatic index (testis wt/total body wt) × 100 of juvenile coho salmon vs. length of fish for July, August, and September 1981–84. Only data for those testes actually weighed are shown.

prised a higher percentage of fish larger than 300 mm FL in August 1981 and larger than 350 mm FL in September 1982, 1983, and 1984. These results indicate that most juvenile coho salmon caught off Oregon and Washington were not sexually precocious. Thus, the relatively large catches of juvenile coho salmon in late summer are explained by lack of strong migrational tendencies of juvenile coho salmon in this region and not by a high proportion of precocious "jacks" that resided in this region as a prelude to re-entry of streams for spawning.

TABLE 4.—The percent of coho salmon jacks and males, by length groups, in the total catch, August 1981 and September 1982–84.

Date	Fork length (mm)	Number of fish examined	% males	Number of jacks[1]	Total catch	Est. total jacks	Est. % jacks of total
Aug. 1981	<200	71	60.6	0	111	0	0
	201–250	63	60.0	1	115	2	1.7
	251–300	55	47.3	4	104	8	7.7
	301–350	16	81.3	4	22	6	27.3
	351–420	10	80.0	8	19	15	78.9
	Total	215	59.5	17	371	31	8.4
Sept. 1982	<200	56	55.4	0	125	0	0
	201–250	21	76.2	0	54	0	0
	251–300	22	63.6	0	109	0	0
	301–350	33	69.7	3	97	9	9.3
	351–420	13	53.8	5	28	11	39.3
	Total	145	62.8	8	413	20	4.8
Sept. 1983	<200	16	62.5	0	18	0	0
	201–250	23	47.8	0	25	0	0
	251–300	23	56.5	0	71	0	0
	301–350	39	61.5	4	77	8	10.4
	351–420	2	0	1	3	2	66.7
	Total	103	58.3	5	194	10	5.2
Sept. 1984	<200	6	33.3	0	15	0	0
	201–250	38	47.4	0	69	0	0
	251–300	90	50.0	2	128	3	2.3
	301–350	27	55.6	12	31	2	6.5
	351–420	6	33.3	2	7	2	28.6
	Total	167	49.1	16	250	7	2.8

[1]Jack is defined as a male whose testes wt./total body wt. × 100 > 0.3% in August and >2.0% in September.

Movements of Marked Fish

Direct evidence of movements of juvenile coho salmon was obtained from capture of marked fish containing coded wire tags or marked with fluorescent pigment. The generalized pattern of movements that emerges for 1981–85 is an initial movement of most juvenile coho salmon to the south soon after ocean entry in May and June and then a reversal of movement with most fish migrating to the north by August and September (Figs. 4–8). These trends are discussed for fish originating from the Columbia River, Oregon coastal, Washington coastal, and private hatcheries.

Columbia River

Juvenile coho salmon originating from hatcheries on the Columbia River were usually recovered south of the Columbia River in May. This trend was especially obvious in May 1982 when all 22 marked fish which were recovered moved south, some as far as 175 km (Fig. 5). In May 1981, all but one of 14 marked Columbia River fish were caught to the south, three as far as 180 and 204 km (Fig. 4). In May 1983, all four fish were taken south of the mouth of the Columbia River (Fig. 6).

During June and July of all years, marked Columbia River coho salmon were recovered in nearly equal proportions both north and south of the river mouth, except in June 1982 when 15 of 17 fish were found to the south (Figs. 4–8). By September, all marked Columbia River coho salmon were captured north of the river, including fish captured off the Quinault River in September 1982 and off Cape Flattery in September 1984. Fish were also caught close to the mouth of the Columbia River in July, August, and September, indicating that some marked juvenile coho salmon did not undertake extensive migrations at sea.

In two sets on the Wecoma Beach Transect on 1 June 1982 we caught 17 marked juvenile coho salmon released between 30 April and 6 May from six hatcheries on the Columbia River. Based on downstream migration rates for these groups to Jones Beach (Dawley et al. 1985) and assuming similar rates from Jones Beach to the ocean, these fish had probably been in the ocean for <10 days before recapture. This indicates that some juve-

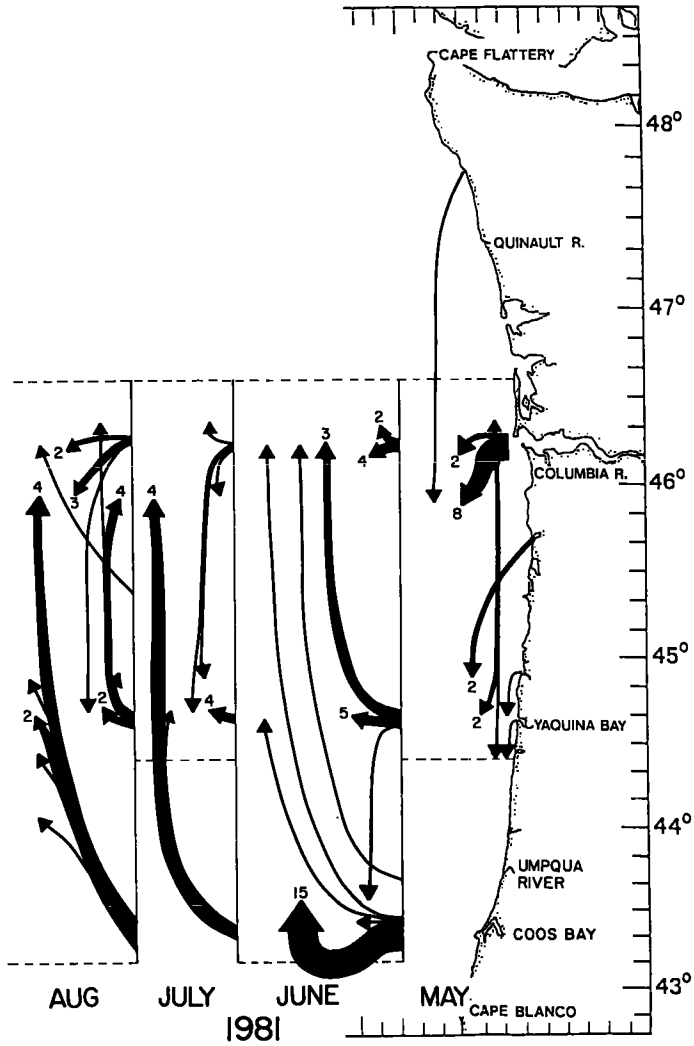

FIGURE 4.—North-south movements of marked juvenile coho salmon captured in purse seines, May–August 1981. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

nile coho salmon released from hatcheries at about the same time tended to stay together during their downstream migration in the Columbia River and during early residency in the ocean.

Oregon Public Coastal Hatcheries

We captured marked fish originating from public Oregon coastal hatcheries both north and south of the latitude of ocean entrance in May. A total of five fish were found to the south, while 11 fish were found to the north in May (Figs. 4–8). With the exception of one coho salmon from the Umpqua River in June 1983 and two from the Rogue River in July 1984 (Figs. 6, 7), the other 25 fish taken after May were captured north of where they entered the ocean. Northerly movements into Washington waters occurred by June 1983 and 1985 (Figs. 6, 8).

The southward movements of two juvenile coho salmon released from the Rogue River (south of Cape Blanco) and captured off northern Califor-

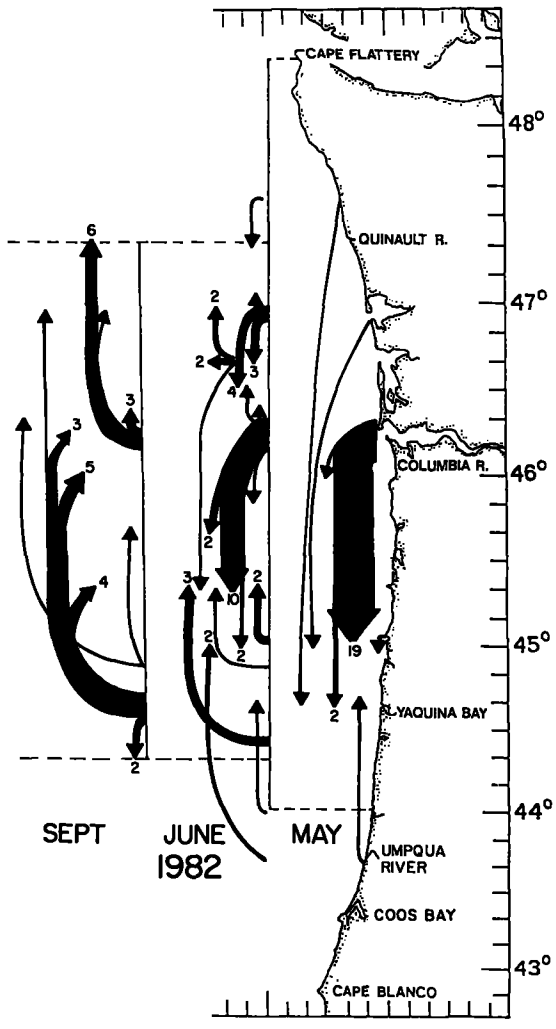

FIGURE 5.—North-south movements of marked juvenile coho salmon captured in purse seines, May, June, and September 1982. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

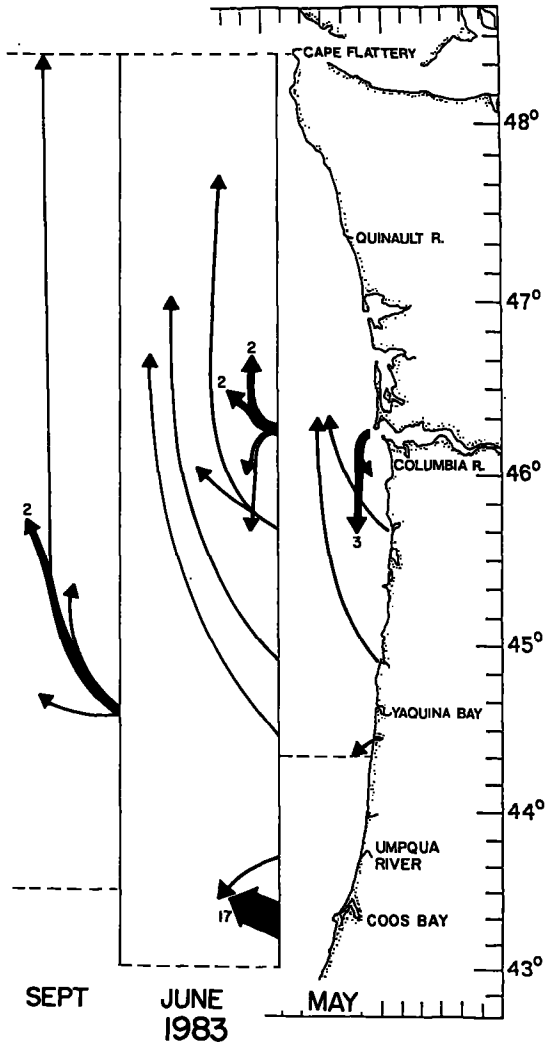

FIGURE 6.—North-south movements of marked juvenile coho salmon captured in purse seines, May, June, and September 1983. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

nia during July 1984 are notable (Fig. 7). They were captured in our only cruise into California waters and represent the only recoveries of marked juvenile coho salmon originating from hatcheries south of Cape Blanco in all six years of sampling. Although ocean sampling was limited south of Coos Bay, if juvenile coho salmon from southern Oregon and northern California hatcheries had migrated north of Coos Bay, we would expect them to be represented in our catches. The fact that they were not caught in this northern region, but two were caught after swimming to the south, suggests that juvenile coho salmon originating in streams south of Cape Blanco may migrate south, possibly occupying the region of intense coastal upwelling off northern California during their first summer in the ocean. The catch of over 70% of the adult coho

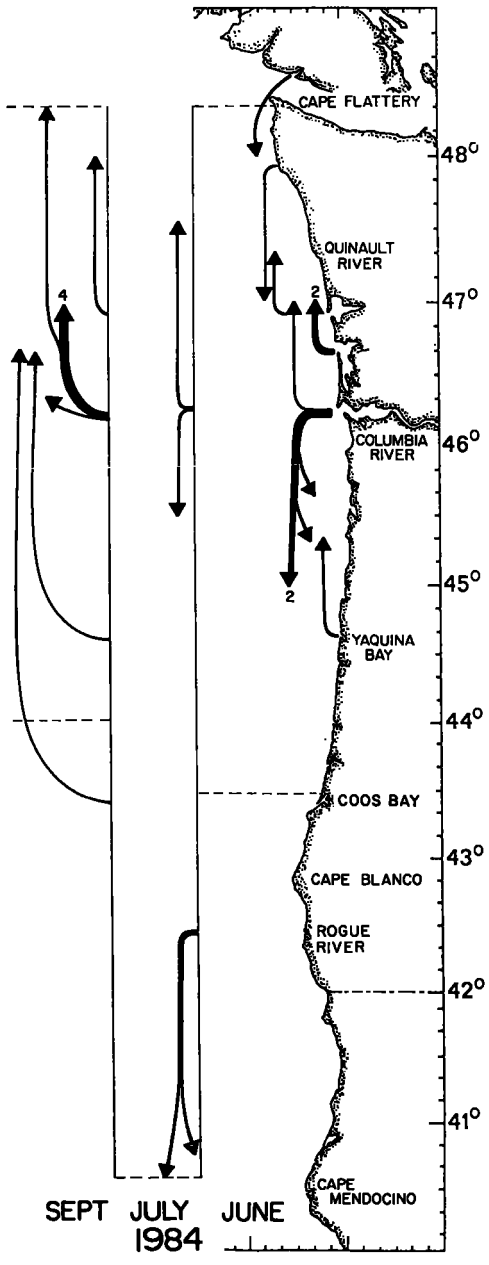

FIGURE 7.—North-south movements of marked juvenile coho salmon captured in purse seines, June–September 1984. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

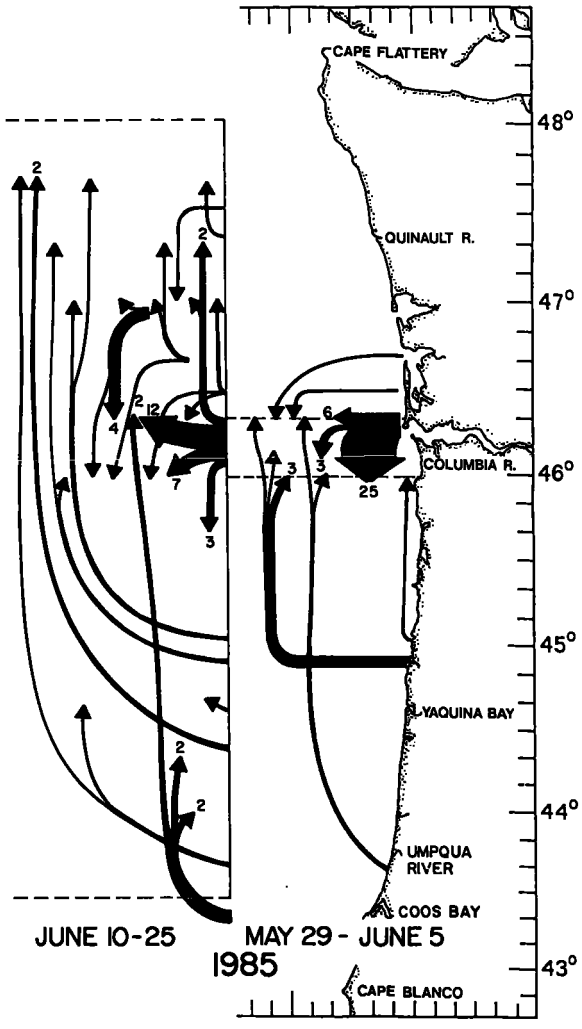

FIGURE 8.—North-south movements of marked juvenile coho salmon captured in purse seines, 29 May–5 June and 10–25 June. The width of the lines are approximately proportional to the number of fish. Numbers at end of arrows indicate number of fish captured. Arrows without numbers and thin lines represent single fish. Inshore-offshore movements are not shown. Dashed lines indicate latitudinal extent of sampling.

salmon from the Rogue River in the troll fishery off California (R. Garrison[3]) is further evidence for a southern distribution of this stock. Marked juvenile coho salmon from California hatcheries were reported from the sports fishery off southern Oregon, however, as will be shown later.

Washington Coastal Hatcheries

Juvenile coho salmon from Washington public hatcheries demonstrated southerly movements, sometimes into Oregon waters, during May 1981 and 1982 (Figs. 4, 5). During June 1982, 1984, and 1985, Washington coastal fish were found both north and south of ocean entry. Except for one fish that moved north in September 1984, no Washington coastal fish were taken in August or September of other years, suggesting that most Washington fish may have migrated out of our sampling area by late summer.

Oregon Private Hatcheries

All marked juvenile coho salmon originating from Yaquina and Coos Bays that we captured at sea were from private hatcheries. Those from Yaquina Bay were mainly age 0.0 smolts from OAF, those from Coos Bay were either age 1.0 smolts from Anadromous, Inc. or age 0.0 smolts from OAF. Forty-one recoveries of marked OAF fish released from Yaquina Bay were caught to the north while only 4 were to the south of Yaquina Bay. In general, more juvenile coho salmon from Yaquina Bay were captured in late than early summer, and distances traveled to the north were largest (up to 413 km) for fish caught in later summer (Figs. 4–8). All recoveries of marked Anadromous, Inc. and OAF fish released into Coos Bay were to the north in all years. Large northerly movements were demonstrated by some of these fish (Figs. 4, 6, 8). Since our sampling in the ocean usually did not extend south of Coos Bay, recoveries of these fish are biased to the north; however, strong northward movements of these stocks were indicated.

Rates of Movement

Recoveries of marked juvenile coho salmon in the ocean provided information on the minimum rates of movement from hatchery release to capture in the ocean. Some fish moved rapidly through estuaries into the ocean. We captured some tag-groups in the ocean only a few days after the median date of capture at Jones Beach (75 km from the ocean) as reported by Dawley et al. (1985): 5 fish after 2 days in 1981, 6 fish after 3–11 days in 1981, 8 fish after 1–14 days in 1982, and 5 fish after 3–8 days in 1983. Dawley et al. (1986) found average rates of movement of 14–23 km d^{-1} for marked groups of coho smolts from areas of release on the Columbia River to river km 75, and rates of movement that were 40% faster from river km 75 to the lower Columbia River estuary and to the ocean plume. These recoveries and those reported by Miller et al. (1983) for yearling chinook salmon and steelhead trout indicate rapid movements of juvenile salmonids of over 20 km d^{-1} through the Columbia River estuary.

Some juvenile coho salmon released from Yaquina Bay and Coos Bay also demonstrated rapid movements into and in the ocean, e.g., 17 Anadromous, Inc. fish were captured 11 km north of Coos Bay only two days after release in June 1983 (Table 5). Myers (1980) described an exponential decrease in the catches of juvenile coho salmon released from the OAF facility into Yaquina Bay; about one-half the fish from marked groups remaining in the bay after 1.7–9.0 days. Juvenile coho salmon apparently emigrate rapidly from estuaries into the ocean.

Some of the marked fish recovered within 10 days of release demonstrated rapid movements down-rivers or in the ocean. Twenty-four fish traversed 10 km d^{-1} or more largely in the ocean, in both north and south directions (Table 5). Four fish released in bays or in the ocean moved over 18.8 km d^{-1}. Two of these swam to the north, presumably against coastal currents. These speeds are equivalent to 1.7 body lengths (BL) per second or more and suggest that some fish must be traveling nearly straight courses during 24-h days, since 1–3 BL s^{-1} are thought to be optimal cruising speeds for small (<20 cm) pelagic fishes (Weihs 1973; Ware 1978). These maximum rates of movement for purse seine caught juvenile coho salmon are similar to those estimated by Hartt (1980) and Hartt and Dell (1986) for tagged sockeye salmon during their first summer in the ocean: 14–27 km d^{-1} for 11 Fraser River fish and 6–14 km d^{-1} for 10 Skeena River fish that were between about 8 and 23 cm in length during the migration period.

[3]R. Garrison, Oregon Department of Fish and Wildlife, Corvallis, OR 97330, pers. commun. December 1983.

TABLE 5.—Release information and mean travel speeds in kilometers per day and body length (BL) per second for CWT and fluorescent-pigment marked age .0 coho salmon recovered in the ocean within 10 days of release. CR = Columbia River; OAF = Oregon Aqua Foods, Inc., (OAF Yaquina is 3.7 km from ocean; OAF Coos is 14 km from the ocean), Anad. = Anadromous Inc. (7.4 km from the ocean).

Year	No.	Release location	Date released	Median days to recovery	Mean FL	Mean km/d	Mean BL/s	Direction of movement
1981	1	Big Cr. (CR)	8 June	3	153	22.2	1.7	S
	1	Tanner Cr. (CR)	6 July	6	138	41.0	3.4	N
	1	OAF Yaquina	11 May	7	140	4.0	0.3	S
	1	OAF Yaquina	12 June	2	124	14.5	1.4	N
	2	Anad. Coos	8 June	9	179	2.3	0.2	N
	2	OAF Yaquina	10–15 June	2	124	3.7	0.3	N
	1	OAF Yaquina	10–15 June	2	123	10.2	1.0	N
	1	OAF Yaquina	10–15 June	2	126	18.8	1.7	N
	11	OAF Coos	5–9 June	10	122	1.9	0.2	N
	1	OAF Yaquina	10–15 June	5	124	24.0	2.2	S
	1	OAF Coos	5–9 June	7	136	20.1	1.7	N
1983	17	Anad. Coos	26 June	2	156	11.2	0.8	N
1984	1	OAF-Offshore	7 June	7	143	11.3	0.9	N
1985	6	Tongue Pt. (CR)	24 May	6	151	9.5	0.7	S
	1	Offshore-22 km	30 May	0.9	134	22.0	1.9	S
	1	Naselle River	20 May	9	143	7.8	0.6	S
	1	Cowlitz River	31 May–6 June	2.5	144	88.0	7.1	N

Effects of Ocean Currents

The tendency for juvenile coho salmon to move to the south early in the summer and to the north later in the summer (Figs. 4–8) may be related to advection of water and the size, orientation, and swimming speeds of fish. Generally, surface currents are to the south off Oregon and Washington in the early summer owing to prevailing northwesterly winds (Hickey 1979; Huyer 1983). Southward flow averaging 17–34 km d^{-1} (Huyer et al. 1975, 1979) has been measured near the surface. May and June are periods of peak outflow of the Columbia River, so fish entering the ocean at this time, especially in the Columbia River plume, may be displaced to the south by advection of surface waters. Southward flow is at a maximum in the coastal jet which is strongest (~22 km d^{-1}) during the spring about 15–20 km from shore (Kundu and Allen 1976; Huyer et al. 1979). Since currents can be equivalent to 1.7 BL s^{-1} for a 15 cm smolt, advection alone could explain the southward movement of most marked Columbia River fish during May and June but not the rapid northward movement of fish during this period (see Figures 4–7).

Coastal Oregon fish were often found to the north in May and June, but these fish were usually substantially larger and generally released much earlier in the spring than Columbia River fish, and were presumably better able to swim against the current. Later in the summer when Columbia River hatchery fish had grown larger, movement was also predominately northward. In August and September southward velocities of surface coastal currents are diminished and the mean may be near zero (Huyer et al. 1975). Northward movements during the summer off Oregon and Washington generally cannot be explained by passive drift and in most years must entail active, oriented swimming.

The northern El Niño of 1982–83, which had severe effects on the growth and survival of adult and jack coho salmon (Pearcy et al. 1985; Johnson 1984; Pearcy and Schoener 1987; Fisher and Pearcy in press), also appeared to affect the distribution of juvenile coho salmon. During September of 1983 nearly all the seine-captured juvenile coho were taken along our northernmost transect, off Cape Flattery, WA (Fig. 2). In other years juvenile coho salmon during late summer were common and more equally distributed from the Columbia River northward. In the summer of 1983 juvenile coho salmon may have moved farther north, or more likely those to the south may have experienced higher mortality, as a result of northerly currents (Huyer and Smith 1985), warm temperatures and low productivity (Pearcy et al. 1985; Chung 1985) that prevailed off Oregon.

Recoveries of CWT Juvenile Fish in Ocean Fisheries

Data on ocean location of landings of juvenile CWT coho salmon reported in sports and commercial fisheries in the ocean along the west coast of North America, 1977–83, provide valuable information on ocean migrations of marked fish, although these data are biased by differences in legal minimum sizes, time and duration of open season, and effort in the different regions. The summary of all years shows that, except for California, most of the recoveries of juvenile coho salmon during their first summer in the ocean were in the general region of their ocean entry location (Table 6). Both the actual number of fish reported and the estimated total numbers (in parentheses) support our earlier conclusion that many juvenile coho salmon off Oregon and Washington are not highly migratory. All (20) of the actual recoveries of marked juvenile coho salmon that were released in southeastern Alaskan waters were from southeastern Alaska. Ninety-seven percent of the recoveries of marked fish released in British Columbia waters were landed in British Columbia; only two were landed in Alaska. Most (86%) marked juvenile fish from Puget Sound hatcheries were caught in the Sound, and more were recovered in British Columbia fisheries (13%) than in coastal Washington fisheries (<1%), probably due to the smaller size limits for coho in British Columbia as well as migratory patterns. Half of the actual numbers of recoveries of juvenile coho salmon liberated into Washington coastal waters were landed in Washington coastal ports, followed by British Columbia (29%) and the Columbia River region (17%). Only one was landed in Alaska and two in Oregon ports (Garibaldi and south). Juvenile coho salmon originating from Columbia River hatcheries had a broader distribution of recoveries in other regions. Only 40% of Columbia River fish were caught in this region, 41% were taken in northern regions, including two (1%) in Alaska. The remaining 19% were captured off Oregon. The majority (73%) of Oregon coastal fish were recovered off Oregon, followed by the Columbia River region, Washington coast, and British Columbia. None was reported from Alaska, but 10 (2%) were from California ports. All marked California fish were recovered from the Columbia River region and farther south. Most (87%) were landed in Oregon. The few recoveries of California fish off California is undoubtedly influenced by the larger size limits in this than other fisheries.

TABLE 6.—Recoveries of coded wire tagged juvenile coho in the ocean fisheries 1977–83. Estimated total numbers are in parentheses.

	Landing area						
Release area	S.E. Alaska	British Columbia[1]	Puget Sound	Washington Coast (Areas 2–4)	Columbia River (Area 1 + Astoria)	Oregon Coast (Garibaldi and south)	California
S.E. Alaska	20 (39)	0	0	0	0	0	0
British Columbia	2 (2)	1,086 (1,735)	24 (90)	2 (8)	0	0	0
Puget Sound	0	201 (729)	1,352 (5,262)	9 (40)	1 (2)	2 (9)	0
Washington Coast	1 (5)	71 (316)	7 (42)	125 (451)	42 (151)	2 (77)	0
Columbia River	2	24 (133)	4 (14)	39 (162)	67 (310)	31 (164)	0
Oregon Coast	0	18 (107)	3 (13)	21 (83)	62 (213)	308 (1,137)	10 (45)
California	0	0	0	0	1 (4)	138 (552)	19 (200)

[1]Sports catches are not expanded. The estimated total number = expanded commercial catch + actual number CWT's recovered in the sports fisheries. Preliminary data.

In general, the legal size limits increased from north to south, which could result in more recoveries of juvenile coho salmon in northern than southern regions. Thus, these data do not provide evidence that a large proportion of juvenile coho salmon from British Columbia and waters to the south made northward migrations into Alaskan waters before or during the commercial and sports salmon seasons. Movements of Washington, Columbia River, and Oregon fish into British Columbian waters were common however.

Hunter (1985) expanded the catches of CWT juvenile coho salmon caught along the west coast of North America during 1978–80 to the total landed plus estimated "drop-off" mortality (fish that were hooked and died without being landed) of both tagged and untagged hatchery groups. Calculations of the percentage returns from different release and recapture areas are similar to ours (Table 6). The highest percentage of returns were from the areas of release for all areas except for California, and a higher proportion of the catches of Washington coastal, Puget Sound, Columbia River, and Oregon coastal stocks were reported north than south of the area of release.

Are Juvenile Coho Highly Migratory?

Based on our observations on movements of marked fish, north-south and seasonal trends in abundance and size, and directional purse seine sets during the summer, we conclude that many juvenile coho salmon from Oregon and Washington coastal streams and the Columbia River are transported by currents to the south in May and June but then migrate north later in the summer. The mean catches per set of yearling coho salmon in August and September are a large fraction of those in June, indicating that in the years studied many juvenile coho salmon in coastal waters of Oregon and Washington were not highly migratory. Moreover, more marked juvenile hatchery coho salmon were caught in ocean fisheries in the region of release than in distant waters. Recoveries of juvenile coho salmon released from hatcheries south of Cape Flattery were rare in northern waters off Alaska and relatively few were recovered in British Columbia (Table 6). In addition, the positive correlation between upwelling off Oregon and survival of hatchery coho salmon from the Columbia River, Oregon, and California (Nickelson 1986) also argues for a close coupling of OPI coho salmon with a local, not a distant, environmental event during the time that year-class survival is determined. All of these trends suggest that most juvenile coho salmon from this area are not highly migratory and that many usually remain in coastal waters near their sites of ocean entry during their first summer in the ocean, and perhaps during their entire ocean life. In years of unfavorable ocean conditions, however, movements may be more extensive or mortality may be higher, as suggested by the very low catches of juvenile coho salmon in purse seine sets south of Cape Flattery during September 1983, the year of the recent strong El Niño.

Although Pacific salmon are renown for their long foraging migrations in the subarctic Pacific, coho salmon demonstrate both nonmigratory and highly migratory behavior. Milne (1950) found immature coho salmon almost year-round in Georgia Strait and concluded that two types of coho salmon exist in British Columbia waters: "ocean" and "inshore" types, the "ocean" type spending most of its ocean life in coastal and offshore waters and the "inshore" type in inside waters such as Georgia Strait. Healey (1978) caught "inshore" juvenile coho salmon in purse seines in Georgia Strait during summer, fall, and winter months. Similarily, large numbers of coho salmon originating from streams of Puget Sound remain in the Sound throughout their marine life (Haw et al. 1967). Young coho salmon have also been found in the winter and spring, many months after seawater entry in Yaquina Bay (Myers 1980) and other Oregon estuaries (J. Nicholas[4]). Hartt and Dell (1986), in their impressive study of juvenile salmonids of the northeastern Pacific during 1956–70, recognized these two migratory patterns of coho salmon. They found juvenile coho salmon in waters off Vancouver Island and in the Strait of Juan de Fuca throughout the summer and fall, and concluded that some coho salmon spend their entire marine life in "inside" waters and make only limited ocean migrations.

What Proportion of Juvenile Coho from Oregon and Washington Migrate North?

The tagging experiments reported by Hartt and Dell (1986) and Godfrey (1965) provide convincing evidence for long-distance migrations of coho

[4]J. Nicholas, Oregon Department of Fish and Wildlife, Corvallis, OR, 97331, pers. commun. May 1986.

salmon during their first summer in the ocean. Based on recoveries of maturing coho salmon that were tagged a year earlier at sea during April–October 1956–70, Hartt and Dell (1986) concluded that juvenile coho salmon from the Columbia River, Oregon, and California may form a large proportion of the coho stocks that migrate north along the coast each summer. Of the 70 recoveries of tagged fish that were released between Kodiak Island and 56°N, 37% were recovered the following year in the area of the Columbia River and Oregon-California; of the 59 recoveries of fish released between 56°N and Cape Flattery, 47% were recovered in these southern regions. In all, 25% of the recoveries were from Oregon-California, 16% from the Columbia River, 14% from Washington, 33% from British Columbia, and 12% from Alaska.

Loeffel and Forster (1970) concluded that patterns of radioactive ^{65}Zn in juvenile coho salmon collected in the northeastern Pacific supported the concept of a northerly migration from Oregon and Washington into the Gulf of Alaska during the summer. They found that juvenile coho salmon captured off the west coast of Vancouver Island in June and July 1967 contained ^{65}Zn, presumably originating from neutron activation of Columbia River water used to cool the nuclear reactors at Hanford, WA. ^{65}Zn levels decreased in fish caught farther to the north (54°42′N–58°24′N) in July–September of 1967. The authors thought the low concentrations in northern samples represented background levels and that fish with relatively high levels of ^{65}Zn had associated with the Columbia River plume and subsequently migrated north from the Oregon-Washington region. They found low ^{65}Zn levels in 1968, however, and no pronounced latitudinal gradients. Furthermore, they reported none of the many finmarked juvenile coho salmon released from Oregon and Washington hatcheries in 1967 and 1968 north of Juan de Fuca Strait. Hence their evidence for northward movements of Columbia River or Oregon-Washington coho salmon was equivocal.

During June and July 1984, research was conducted with the NMFS Auke Bay Laboratory in waters from northern California to southwest Alaska from the FV *Pacific Warwind* and *Bering Sea*, both making round hauls with the same size of purse seine, to sample juvenile coho in waters north of Oregon and Washington: 37 sets were made in coastal waters of British Columbia, and 39 were made in coastal waters and 29 in inland waters (bays, inlets, and fjords) of southeastern Alaska. Of the 371 juvenile coho salmon captured in these regions, 77% were caught in inland waters of southeastern Alaska. The seven CWT juvenile coho salmon captured were all from Alaska inland waters and all originated from Alaska hatcheries (Auke Bay Laboratory 1984a). A later cruise in southeast Alaska by the Auke Bay Laboratory in August 1984 caught eight CWT coho salmon, also all from inland waters and from Alaskan hatcheries (Auke Bay Laboratory 1984b).

Of the 14 CWT juvenile coho salmon collected in other purse seines, gill nets, and special troll gear in waters of southeastern Alaska during 1982, 1983, and 1985, 12 originated from Alaska hatcheries and 2 originated from Washington hatcheries (Auke Bay Laboratory 1983; Jaenicke et al. 1984; Orsi et al. 1987). Table 6 shows that only 5 of 25 CWT juvenile coho salmon caught in Alaskan waters during 1977–83 were from hatcheries south of Alaska, indicating that most juvenile coho salmon caught in southeastern Alaska during the summer originated from Alaska and not from southern regions.

Hartt (1980) and Hartt and Dell (1986) recognized that their data did not indicate the proportion of southern stocks that made northerly migrations, but they concluded that a large proportion is probable, since juvenile coho salmon were consistently caught in most seine sets throughout the area sampled. They estimated that the average density of juvenile salmonids in coastal waters between 56°N and 60°N off southeastern Alaska during August and September 1964–68 was 1,500 km^{-2}. The average density of juvenile coho salmon in this area during these two months was only 82 km^{-2} (Hartt and Dell 1986, app. A). During August and September 1981–84, the average density of juvenile coho salmon in our round hauls between Cape Flattery, WA and Cape Arago, OR to 37 km offshore was 350 km^{-2}, several times the estimates of Hartt and Dell for the same months of the year. This suggests that juvenile coho salmon may be found in higher densities off Oregon and Washington than southeastern Alaska during late summer, assuming that distributions and abundances in the late 1960s and early 1980s were similar. This trend for higher abundances of juvenile coho salmon off Oregon and Washington than in coastal waters farther north was also found during July 1984 (Table 7), although average catches off Washington and Oregon were not as

TABLE 7.—Average catches of juvenile coho salmon in purse seines sets in coastal waters along the west coast of North America during July 1984[1,2]

Area	No. per set	No. per km^2
Sitka-Juneau	1.29	68
Ketchikan-Sitka	0.58	3
Cape Scott-Dixon Entrance	1.90	100
Vancouver Is.	1.80	95
Washington	3.76	198
Oregon/No. California	2.59	136

[1]Cruise Report, Drum Seiner FV *Bering Sea*, Coastwide NWAFC/OSU Cooperative Study, Ecology of Juvenile Salmon in Coastal and Inside Waters of Southeast Alaska, 28 June–26 July 1984. NWAFC Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 115, Auke Bay, AK 99821.
[2]Fisher and Pearcy (1984).

large as in some earlier years owing to low survival (Fig. 2; Pearcy 1984; Fisher and Pearcy in press).

Comparisons of the estimates of total juvenile yearling coho salmon abundances off Oregon and Washington with the production of coho smolts in the Oregon Production Area (Columbia River to California) also suggests that many juvenile coho resided off Oregon and Washington during the summer. By expanding our catches per m^2 to the region sampled, we estimated that the numbers of juvenile yearling coho salmon in areas surveyed by our purse seine sampling during August or September 1981–84 were 6.3%, 6.5% 5.1%, and 5.2%, respectively, of the numbers of hatchery and wild smolts released in the Columbia River and in Oregon (T. Lichatowich[5]). The areas included in these estimates were roughly 83%, 62%, 51%, and 68% of the total area from Cape Flattery to Cape Arago out to 37 km offshore. Recognizing that the entire area was not sampled, that year-class strength of coho salmon in this region is probably established soon after ocean entrance (Fisher and Pearcy in press), and that early marine mortality may be inversely related to size (Parker 1968; Ricker 1976) so that much of the ocean mortality has occurred by late summer, these percentages probably represent a substantial portion of the surviving OPI coho smolts. In fact, they are several times higher than the smolt-to-adult survival of 1.3–2.8% for OPI public hatchery coho salmon (excluding Rogue River and California hatcheries) during 1981–84 (R. Kaiser[6]).

We conclude, therefore, that a major fraction of the juvenile coho salmon from Oregon and Washington hatcheries did not undertake distant migrations into the Gulf of Alaska in recent years. This is not necessarily in conflict with Hartt and Dell's (1986) data, since they established the presence of Oregon and Washington coho salmon in northern waters but not the proportion of total production that undertakes this migration. On the other hand, neither the stocks of coho nor oceanographic conditions have remained constant over the period from 1956 to 1985 when these two studies were conducted. Wild coho smolts exceeded hatchery smolts in the Oregon Production Area before 1961 (Nickelson 1986) but comprised <12% of the smolts in 1980–85 (R. Kaiser fn. 6). Perhaps wild smolts from the OPI area had different migratory patterns than hatchery smolts do today and migrated rapidly into northern waters soon after ocean entrance. This may explain Nickelson's (1986) finding that survival of hatchery, but not wild coho smolts, was significantly correlated with coastal upwelling off Oregon.

Ocean conditions have also changed over this period. The late 1960's were accompanied by strong upwelling along the coast compared to weak upwelling in the early 1980's (Nickelson 1986; Mason and Bakun 1986). McLain (1984), Norton et al. (1985), and Royer (1985) illustrated that sea surface temperatures and sea levels increased in the northeastern Pacific between 1976 and 1984. These factors and associated changes in ocean circulation could explain differences in migratory behavior of coho salmon between 1960's and 1980's. If currents provide orientational cues to migration, cues facilitating northerly movements may be reduced during years of weak upwelling and weak Ekman transport from the north. Ocean conditions may have modified migratory patterns, as they possibly have for the migration of Fraser River sockeye salmon around Vancouver Island (Groot et al. 1984; Hamilton 1985).

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[5]T. Lichatowich, Oregon Department of Fish and Wildlife, P.O. Box 59, Portland, OR 97207, pers. commun. September 1987.
[6]R. Kaiser, Oregon Department of Fish and Wildlife, Hatfield Marine Science Center, Newport, OR 97265, pers. commun. September 1987.

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EARLY MARINE LIFE OF ATLANTIC SALMON, *SALMO SALAR*, POSTSMOLTS IN THE NORTHERN GULF OF ST. LAWRENCE

J.-D. DUTIL AND J.-M. COUTU[1]

ABSTRACT

Postsmolts of Atlantic salmon, *Salmo salar*, having spent some 2–4 months in the marine environment were collected in the nearshore zone of the northern Gulf of St. Lawrence. From a back-calculated smolt length of 135 mm they had increased in length to 265 mm (212 g) on 1 September, and 306 mm (320 g) on 30 September. The rate of increase in length averaged 1.65 mm/day over more than 2 months. Individuals reached 35 cm and 500 g in late autumn. Postsmolts moved in small shoals near the surface and were possibly more active at dawn and dusk. In midsummer, stomach contents changed from insects and gammarids to sand lance, 40–100 mm in length; vertically migrating crustaceans also occurred in the stomachs in autumn. River origin of these postsmolts is not known. The possibility of their belonging to a particular subgroup of some north shore stocks is examined in relation to scale patterns and size of gonads. This occurrence of postsmolts near shore in late summer and presumably their late movement out of the Gulf of St. Lawrence indicate the directional nature of smolt migration to distant feeding areas should be reconsidered. Low sea temperature is hypothesized to trigger the movement out of the Gulf of St. Lawrence. Continual presence of postsmolts in a shallow layer at the surface could prove to be extremely valuable in forcasting movements and production.

Many papers have been published concerning the biology of Atlantic salmon, *Salmo salar*, but very little has been said concerning the postsmolt stage. This stage has been defined as ". . .the juvenile salmon from the time that it leaves the river as a smolt until the onset of wide annulus formation on the scales at the end of the first winter in the sea" (Allan and Ritter 1977). This paper presents new data on the Atlantic salmon postsmolts (hereafter referred as postsmolts) in the northern Gulf of St. Lawrence, reviews our current knowledge on the biology of postsmolts, and points to biological and environmental factors potentially limiting the success of their early life in marine environments.

Published data on postsmolts are mainly limited to stocks in the Baltic Sea. Routes of migration have been described based on the locations and time of early recapture from smolt releases in Sweden and Finland (Carlin 1959; Larsson and Ateshkar 1979; Ikonen and Auvinen 1984, 1985; Jutila and Alapassi 1985). Data on predators are limited (Soikkeli 1973; Valle 1985), and most of the material concerns predation on smolts in streams and estuaries (Larsson 1985). Many analyses of stomach contents have been published, particularly on smaller postsmolts (reviewed by Christensen and Larsson 1979; Jutila and Toivonen 1985). Data on rate of growth (Ikonen and Auvinen 1985) and rate of mortality (Carlin 1959) are lacking. However, Baltic salmon spend their entire sea life in the brackish waters of the Baltic and nearly 80% of smolt production originates from hatcheries (Anonymous 1984). Thus the information derived from salmon in the Baltic should be extended to other stocks only with caution.

Publications on postsmolts in the northern Atlantic and Gulf of St. Lawrence mentioned small salmon as bycatches of commercial fisheries and described the distribution of recaptures from smolt release programs. The earliest report on postsmolts in the Gulf of St. Lawrence claimed that small salmon, referred to as "ouananiche" by local fishermen, were regularly taken near shore in herring nets in autumn (Comeau 1909). Kendall (1935) also reported such incidental catches for the New England coast. Elson (1953) recorded a bycatch of more than 1,000 marked postsmolts from one locality in the Bay of Fundy in the period 1951–53 and reported their mean length. There are also limited records of postsmolts taken off France (Vibert 1953) and in the Gulf of St. Lawrence (Caron 1983) from smolts tagged in streams. Recently, information on movements has been derived from tag returns

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of smolts released in spring in New England and caught in summer in Canada (Meister 1984). Rumors of bycatch in herring nets along the coast of the northern Gulf of St. Lawrence in autumn provided an occasion to acquire some knowledge concerning the elusive postsmolt. Production of salmon in the sea may well be limited by the success of smolts in the marine environment.

Materials and Methods

Postsmolts were collected between Baie Trinité and Rivière-au-Tonnerre in the northern Gulf of St. Lawrence, in 1982, 1983, 1984, and 1985 (Fig. 1). Fishermen contacted in summer 1982 collected postsmolts in late summer and autumn as bycatch in herring gill nets. Four of them were asked in 1983 to monitor the catch of postsmolts in experimental gill nets in late-September in 4 locations (Baie Trinité, Rivière Pentecôte, Port Cartier, and Sept-Iles). We also monitored stations in Baie Trinité in 1983 (23 September–11 October), in Baie Trinité and Port Cartier in 1984 (21 August–20 October), and in Sept-Iles in 1985 (20 August–4 October). Finally, smolts and early postsmolts were collected in seines in June and July, during an eel marking program in the estuary of Grande Trinité River at Baie Trinité (Fig. 1).

Fishermen used standard herring gill nets in 1982, but custom-made gill nets were used in 1983, 1984, and 1985. Custom-made gill nets had 5 sections of increasing mesh sizes (50.8, 57.2, 63.5, 69.9, and 76.2 mm stretched) covering the range in mesh sizes of herring gill nets in the northern Gulf of St. Lawrence. Stretched mesh sizes were determined by measuring 10 meshes per section. Sections were 6 m deep and 10 m long. In 1983, 1984, and 1985, postsmolts were recorded by section individually. In 1984 and 1985, their position in the nets was recorded more precisely: floating lines had numbered buoys and a string divided the nets into 2 halves horizontally. Time of the catch was also recorded. The gill nets were usually visited at 2-h intervals between 0600 and 1800, as sea conditions allowed. They were left fishing overnight. Gill nets were all set at the surface and near shore (<2 km). Mean air temperatures for 1982 to 1985 were drawn from Environment Canada meteorological summaries for Sept-Iles airport. Temperature recorders were also tied to nets in 1983, 1984, and

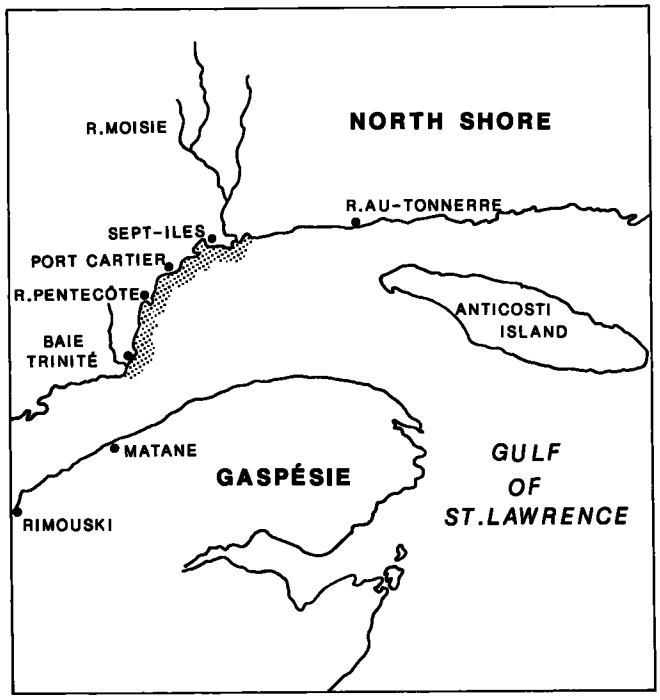

FIGURE 1.—Locations of the areas investigated in the northern Gulf of St. Lawrence (shaded area).

1985 to get hourly records of temperature near the surface, but portions of these records are missing.

Fish were preserved at −15°C for less than 4 months in 1982 and less than 2 months in 1983, 1984, and 1985. Fork length was measured to nearest mm and weight to nearest g. Condition index values were calculated as

$$CI = \sin^{-1}\left[\frac{100 \cdot W}{L^s}\right]^{0.5}$$

CI = condition index; W = weight (g); L = length (mm); s = slope of the length-weight relationship for age groups combined. Scales, usually taken below the dorsal fin close to the lateral line, were cleaned and mounted on glass slides. Stomachs were preserved in formalin (10%) or alcohol (70%) to be analyzed later for their contents. The sex was determined visually and checked histologically on a subsample of postsmolts collected in 1982. Gonads were weighed to nearest mg and only in 1982. Gonadosomatic index (GSI) was calculated as

$$\text{GSI} = \frac{\text{GW}}{\text{TW} - \text{GW}} \cdot 100$$

where GW = gonad weight; TW = total weight.

Scales showing no focal regeneration were examined for age determination by 2–4 readers. Readings were discussed and a consensus was reached in most cases. Reported ages are smolt ages plus 2–4 months. Fork length at smoltification (mm) was back-calculated as

$$\text{LS} = \left[\frac{(\text{LC} - 34) \cdot \text{RS}}{\text{RC}}\right] + 34$$

where LS = back-calculated smolt length; LC = body length of post smolt; RS = scale radius at smolt check; RC = scale radius of postsmolt. Length at scale formation is assumed to be 34 mm. Scales were also examined for any mark in the postsmolt zone that could be of potential interest. Hence the number of individuals showing a transition zone between the riverine and marine increments was determined in 1982, and the number of individuals showing a summer check was determined in 1982, 1983, 1984, and 1985. Scale radii were measured along the postero-anterior axis on 4 scales per individual in 1982, and on 1 scale per individual in 1983, 1984, and 1985. Projected scales were measured at constant magnification on a digitizing pad connected to a personal computer. Fork length at formation of a summer check (mm) was back-calculated for 1982 and 1983 as

$$\text{LF} = \left[\frac{(\text{LC} - 34) \cdot \text{RM}}{\text{RC}}\right] + 34$$

where LF = back-calculated length; LC = body length of postsmolt; RM = scale radius at summer check; RC = scale radius of postsmolt.

Stomach contents were examined in detail in 1982. Results are expressed as percentage of occurrence (number of stomachs containing an item divided by the number of stomachs examined) and percentage by number (the count number of an item divided by the count number of all items). Food items that could not be identified are referred to as remains. In as far as their condition allowed, prey fish were usually measured to the nearest cm. Stomach contents examined in 1983, 1984, and 1985 were consistent with the 1982 conclusions, so the results are not presented.

Results

The Age and Sex Composition

Three-year-old female salmon dominated the catch both in 1982 and 1983 (Table 1). Postsmolts ranged from 2 to 5 years in 1982 and from 2 to 4 years in 1983. Five-year-old salmon made up less than 4% of the catch in 1982. Three-year-old and, to a lesser extent, 4-yr-old salmon dominated the catch both in 1982 and 1983 (82% of the catch); mean smolt age was 3.2 ± 0.7 years. Age composition in 1983 differed from 1982 because of an increase in the percentage of 2-yr-old salmon (12% to 21%) and a decrease in the percentage of 5-yr-old salmon ($\chi^2 = 15.96$, $P < 0.01$). The sex ratio (male:female) for 1982 and 1983 combined was

TABLE 1.—The age and sex composition of the catch of postsmolt Atlantic salmon along the north shore of the Gulf of St. Lawrence, 1982 and 1983.

		Smolt age				
Year	Sex	2	3	4	5	Total
1982	Female	26	114	79	7	226
	Male	19	67	49	7	142
1983	Female	25	58	15	0	98
	Male	8	26	23	0	57
Total	Female	51	172	94	7	324
	Male	27	93	72	7	199

0.62. This ratio did not change between years ($\chi^2 = 7.92$, $P < 0.01$) and was significantly less than 1.0 (binomial test: $z = -5.37$, $P < 0.001$). There was no trend between sex ratio and smolt age in 1982 ($\chi^2 = 1.21$, $P = 0.75$), but the percentage of males tended to increase with smolt age in 1983 ($\chi^2 = 12.67$, $P = 0.002$).

Length at Smoltification

The mean length at smoltification was estimated by back-calculation at 135 ± 15 mm for postsmolts collected in 1982 and 1983. Scale radius was linearly related to body length both in 1982 (4 scales measured per fish, $P < 0.0001$) and in 1983 (1 scale measured per fish, $P < 0.0001$); probability values are those of F-tests from analysis of variance. Back-calculated smolt lengths were normally distributed ($P = 0.80$): 75% of the postsmolts ranged between 120 and 150 mm at smoltification. There were also 7% individuals in the 160–200 mm range. Differences in mean smolt length were not significant between the ages and the sexes both in 1982 ($F = 1.84$, $P = 0.08$) and in 1983 ($F = 1.05$, $P = 0.39$), and, pooling the ages and the sexes, between 1982 and 1983 ($t = 1.32$, $P > 0.15$).

Rate of Increase in Size

The rate of increase in size of postsmolts was very rapid in summer both in 1982 and 1983. Postsmolts collected in 1982 between mid-August and mid-October ($n = 383$; mean date is 1 September) averaged 265 ± 25 mm (range 195–328) and 212 ± 58 g (range 92–389). In 1983, postsmolts collected between mid-September and mid-October ($n = 155$, mean date is 30 September) averaged 306 ± 17 mm (range 258–362) and 320 ± 57 g (range 192–565). There was no difference in mean size between males and females and between age-classes in 1982 ($P > 0.40$) and 1983 ($P > 0.20$); probability values are those of F-tests from 2-way analysis of variance. From a mean smolt length of 135 mm and assuming smolts migrated to estuaries 15 June, postsmolts grew at a rate of 1.65 mm/day during a 2.5-mo (15 June—1 September) and a 3.5-mo (15 June–30 September) period in 1982 and 1983, respectively.

This estimate is conservative because the rate of increase in length tended to decrease late in the sampling period. Postsmolts steadily increased in length and weight in the period mid-August to mid-September 1982 (Figs. 2, 3). From mid-September, the rate tended to slow down. The inclusion of data for 1983, collected later in the autumn, corroborates this observation indicating that conditions changed in late-September in 1982 and 1983.

Length-weight relationships were examined for 1982 and 1983 separately. The analysis of covariance showed that males and females exhibited the same length-weight relationship, both in 1982 ($P = 0.53$) and 1983 ($P = 0.42$). Similarly, length-weight relationship did not change between age groups in 1982 ($P = 0.06$) and 1983 ($P = 0.49$). The covariance for 1982 was nearly significant because the slope for 5-yr-old postsmolts, based on 15 individuals, was larger than for other age groups. However, mean condition index values by age revealed no significant difference between age groups in 1982 ($P = 0.11$) or 1983 ($P = 0.28$).

Since there was also no significant difference in the length-weight relationship between 1982 and 1983 ($P = 0.14$), the data were pooled. Thus the length-weight relationship for postsmolts collected in this study can be described as a single regression:

$$\log W = (2.8280 \cdot \log L) - 4.5336$$

$$P < 0.001,\ n = 539$$

where W = weight (g); L = length (mm).

Maturation of Gonads

Postsmolts were all immature both in 1982 and 1983, but differences were observed between males and females in 1982. Testes averaged 48 ± 6 mg (95% C.L., $n = 124$) for a mean male gonadosomatic index value of 0.025% ± 0.003% (95% C.L., $n = 124$). There was no significant difference in the mean value of either parameter between age groups ($P > 0.52$). Testis weight increased in time and as body length and body weight increased, but again there was no difference between age groups (Table 2). However, the gonadosomatic index did not change in time ($P = 0.10$) or as postsmolts' size increased ($P = 0.16$ for body length and $P = 0.10$ for body weight), suggesting that changes in size of the testes were not allometric in male postsmolts in the autumn period. Regressions were tested and compared following Snedecor and Cochran (1967) and Sokal and Rohlf (1969).

There was more variability in the data for fe-

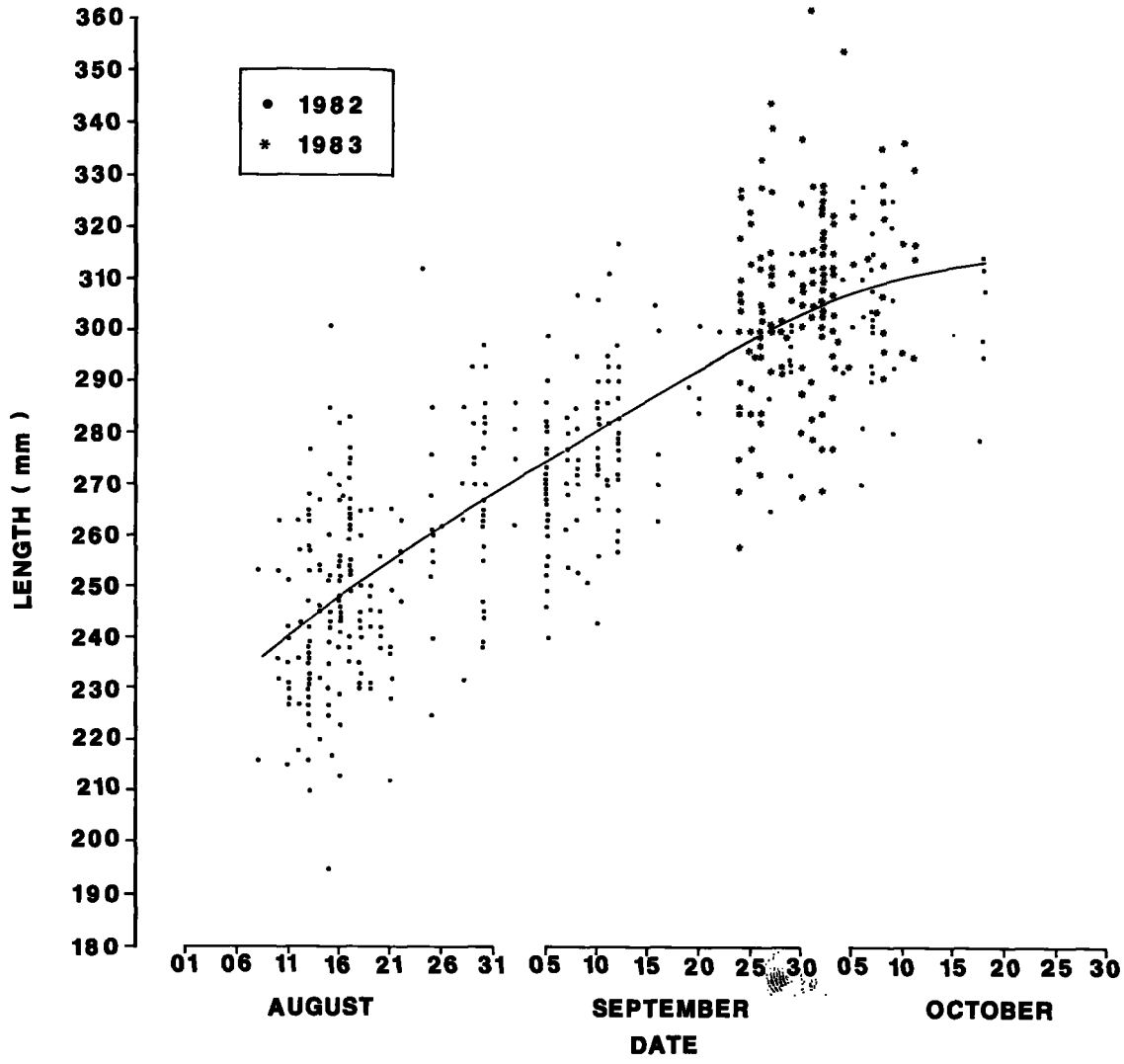

FIGURE 2.—Seasonal changes in length of Atlantic salmon postsmolts collected in 1982 and 1983.

TABLE 2.—Functional regressions of gonad weight on date, body length, and body weight of Atlantic salmon male postsmolts (n = 124). Lengths and weights are log-transformed.

	Date	Length (mm)	Weight (g)
Regression	$P < 0.0001$[1]	$P < 0.0001$[2]	$P < 0.0001$[3]
Covariance (age groups)	$P = 0.31$ n.s.	$P = 0.56$ n.s.	$P = 0.47$ n.s.

[1] $Y = 0.0168\ X - 5.4166$.
[2] $Y = 7.8496\ X - 20.3350$.
[3] $Y = 2.6798\ X - 7.5298$.

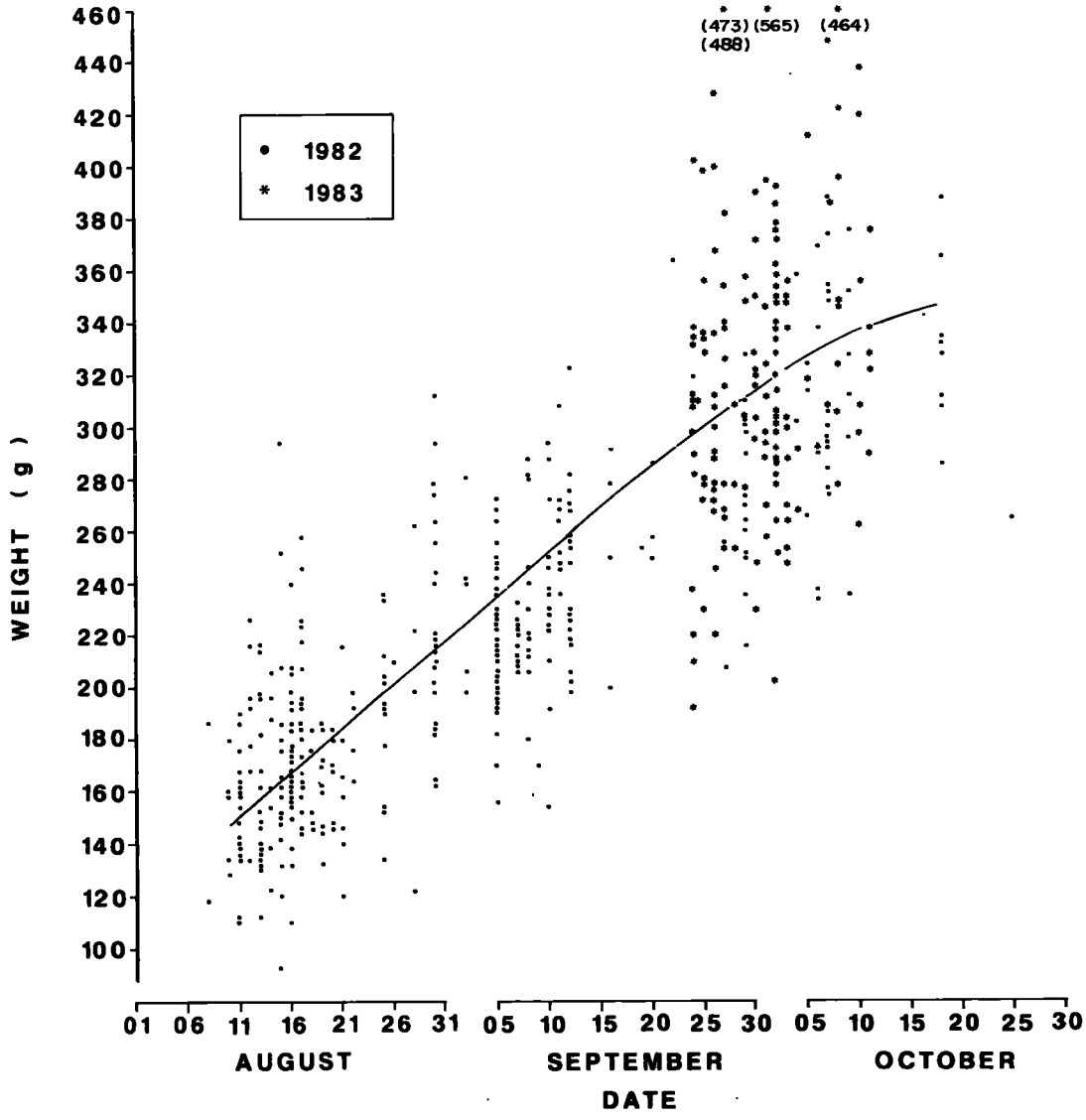

FIGURE 3.—Seasonal changes in weight of Atlantic salmon postsmolts collected in 1982 and 1983.

males. Though the size of ovaries did not differ significantly between age groups ($P = 0.07$), gonadosomatic index values increased in older female postsmolts ($P = 0.0006$). Mean values ranged from 133 mg (0.06%) for 2-yr-old postsmolts to 205 mg (0.10%) for 5-yr-old postsmolts (Table 3). The regressions of ovary weight on body length, body weight, and time were all significant except for 5-yr-old females (Table 4), and differed between age groups particularly in elevation ($P < 0.05$, $n = 213$). The regressions of gonadosomatic index values on the same variables were

TABLE 3.—Gonad weight (mg) and gonadosomatic index (GSI) (%) of Atlantic salmon female postsmolts: mean values and confidence limits ($n = 213$).

Age group	Gonad weight		GSI	
	Mean	95% C.L. interval	Mean	95% C.L. interval
2	133	124–144	0.064	0.060–0.067
3	152	142–163	0.077	0.073–0.082
4	175	161–189	0.092	0.087–0.098
5	205	194–217	0.095	0.091–0.099

not significant indicating that, in females as in males, changes in size of the gonads were not allometric (body length: $P = 0.06$; body weight: $P = 0.73$; time: $P = 0.68$).

Scale Marks

Scales used for age determination were also examined for any mark that could be of use in stock identification. Many individuals exhibited a transition zone on their scales. Circuli in this zone were more wide-spaced than circuli laid down in earlier summers, but they were more narrow-spaced than circuli formed in summer in a marine environment. This mark was present on 73% of the scales in both males and females (72.6 and 73.8%) but tended to decrease as smolt age increased: 84% (age 2 years), 75% (3 years), 68% (4 years), and 62% (5 years). However, the trend was not significant ($\chi^2 = 5.74$, $P > 0.10$).

Scales also exhibited summer checks in 1982, 1983, and 1984. The number of circuli between the smolt mark and the summer check was 10.9 ± 2.6 (mean ± SD) (range 7–15) in 1982 and 9.7 ± 2.2 (range 5–15) in 1983. The ratio between the radius to summer check and the radius to smolt mark averaged 2.00 ± 0.30 (range 1.49–2.45) in 1982, and 1.67 ± 0.19 (range 1.26–2.32) in 1983. The overall percentage of occurrence was low in 1982 (3.6%) and involved only specimens collected in the area Baie Trinité-Pointe aux Anglais where 11 out of 13 postsmolts examined showed a summer check. The incidence of summer checks on scales increased markedly in 1983 (55%) and 1984 (75%), and summer checks were no longer restricted in distribution. Examination of data concerning postsmolts possessing a summer check showed no relationship between the check and measured biological variables except perhaps in 1982. The gonads of males having a summer check on their scales ($n = 5$) were heavier than in males having no summer check (120 mg and 48 mg respectively). Their gonadosomatic index was also higher (GSI = 0.042% and 0.025% respectively). This was not so in females. Information on gonads is not available for 1983, 1984, and 1985.

Back-calculated lengths at summer check formation were larger in 1982: 22 ± 2.5 cm in 1982 and 20 ± 2 cm in 1983. Postsmolts measured 265 mm on 1 September. With a mean rate of increase in length of 1.65 mm/day, the check must have been formed some 26 (1982) to 40 (1983) days earlier, i.e., in late-July. This is confirmed by extrapolation of the length-date plot (Fig. 2). No salmon were noted possessing 2 summer checks on their scales.

Food Items

Drastic changes took place in prey selection between postsmolts collected in summer and in autumn. The stomach contents of 40 salmon ranging up to 188 mm in length (70 g) collected in the second half of July 1984 in the estuary of the Grande Trinité River, near Baie Trinité, revealed a low diversity in prey items, indicative of a transition period between the riverine and marine environment. Small fish remains were observed in only 5 out of 39 stomachs containing food remains. Invertebrates were observed in 38 stomachs, classes Insecta and Crustacea occurring in 87 and 92% of the stomachs respectively. Food items consisted mainly of 2 families: Chironomi-

TABLE 4. – Functional regressions of gonad weight on date, body length, and body weight of Atlantic salmon female postsmolts ($n = 213$). Lengths and weights are log-transformed.

	Significance	Functional regression
Date	2 : $P = 0.0001$	$Y = 0.0075\ X - 2.7127$
	3 : $P = 0.0001$	$Y = 0.0044\ X - 1.9052$
	4 : $P = 0.0058$	$Y = 0.0052\ X - 2.0229$
	5 : $P = 0.26$ n.s.	
	covariance : $P = 0.04$	
Length (mm)	2 : $P < 0.0001$	$Y = 3.8015\ X - 10.1089$
	3 : $P < 0.0001$	$Y = 2.9105\ X - 7.8659$
	4 : $P < 0.0001$	$Y = 3.1893\ X - 8.4701$
	5 : $P = 0.34$ n.s.	
	covariance : $P = 0.02$	
Weight (g)	2 : $P < 0.0001$	$Y = 1.3110\ X - 3.9428$
	3 : $P < 0.0001$	$Y = 1.0385\ X - 3.2227$
	4 : $P < 0.0001$	$Y = 1.1763\ X - 3.4659$
	5 : $P = 0.28$ n.s.	
	covariance : $P = 0.04$	

dae (95% of insects by number) and Gammaridae (92% of crustaceans by number).

Later in summer and autumn, postsmolts consumed mainly small fish. Stomach contents were analyzed for 373 out of 385 postsmolts collected in 1982. There were 109 stomachs with no food remains (29%). They were most prevalent in the first half of August: 46%, 1–15 August; 25%, 16–31 August; 26%, 1–15 September; 25%, 16 September–31 October. Fishes dominated the list of prey items as they occurred in 238 out of 264 (90%) stomachs containing food remains, including 200 postsmolts (84%) that fed exclusively on small fish. Fishes could be identified in 157 stomachs. Diversity was low, capelin, *Mallotus villosus*, occurring in 16 stomachs (10%) and sand lance, *Ammodytes americanus*, in 145 stomachs (92%). *Ammodytes americanus* dominated in terms of percentage by number (94%). Postsmolts consumed smaller *A. americanus*, in the 40–100 mm range (Fig. 4). Stomachs examined in 1983, 1984, and 1985 confirmed these observations.

Invertebrates were found in 69 out of 264 stomachs (26%) containing food remains. Eighteen postsmolts had only invertebrates in their stomachs (26%). In contrast with smolts in the estuarine environment, postsmolts did not rely on insects; insects occurred in only 8 stomachs (3%), whereas crustaceans occurred in 61 stomachs (23%) (respectively, 12 and 88% by number). Furthermore, the class Amphipoda no longer dominated the crustaceans (Table 5).

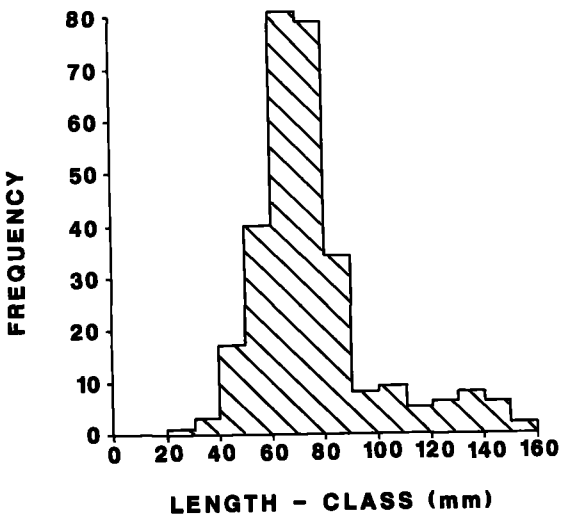

FIGURE 4.—Length distribution of sand lance in the stomachs of Atlantic salmon postsmolts collected in 1982.

Horizontal and Vertical Position in the Nets

Postsmolts were not randomly distributed in the nets in 1984. They occurred most frequently (78% of the individuals) in the top half of the nets (binomial test; $z = 4.62$, $P < 0.001$; Siegel 1956). Furthermore, 25 out of 74 salmon occurred alone in the nets, but many also occurred in clusters. Positions of postsmolts are indicated by number of nearest buoy on the head-line for those sets having taken 2 salmon and more (stations visited at 2-h intervals usually but also nets set overnight) (Table 6). Distributions are likely not random in sets 3, 6, 7, 9, 10, and 11 and most particularly in sets 13 and 15. The catch was low in midday: 3 salmon between 0900 and 1200 and 5 between 1200 and 1500. This increased to 12 between 1500 and 1800. The majority were caught later than 1800 (36) and in the morning between 0600 and 0900 (20).

Finally, positions in the nets were analyzed in terms of selectivity. The gear used in 1982 could not be controlled. Fishermen reported using

TABLE 5.—Crustacean organisms in the stomachs of Atlantic salmon postsmolts collected in the period August–October 1982, based on 39 stomachs containing identifiable crustaceans.

Crustacean order	Percentage of occurrence	Percentage by number	Main organisms
Euphausiacea	87	68	*Meganyctiphanes norvegica* *Thysanoessa inermis* *Thysanoessa raschi*
Decapoda	28	24	*Chionoecetes opilio* (larvae)
Amphipoda	15	8	

TABLE 6.—Positions of Atlantic salmon postsmolts in nets by number of nearest buoy on head-line for catches of 2 salmon and more.

Set no.	No. of smolts	Number of nearest buoy to each smolt								
1	2	11	32							
2	2	12	23							
3	2	14	15							
4	2	15	23							
5	2	19	27							
6	2	22	24							
7	2	23	23							
8	2	23	39							
9	2	25	27							
10	2	23	27	27						
11	4	16	21	21	43					
12	5	16	24	33	42	44				
13	5	23	23	23	23	23				
14	6	12	17	18	18	22	42			
15	9	11	12	12	12	13	13	13	14	14

62 mm stretched mesh nets (range 57–70 mm); mesh size is regulated. The nets used in 1983, 1984, and 1985, had 5 sections of increasing stretched mesh sizes: 50.8, 57.2, 63.5, 69.9, and 76.2 mm. Catches were recorded for individual mesh sizes in 1983 combining the 4 stations. Modal length increased only slightly as mesh size increased. Furthermore, the distribution for the 69.9 mm mesh was skewed to the right, indicating no larger sized postsmolts were present. There was also no catch in the 50.8 mm mesh, but this may have been because of the small mesh section being made of a coarser material in 1983. Postsmolts were frequent (n = 49) in the 57.2 mm mesh, but the distribution for this mesh does not suggest the existence of smaller postsmolts as the size range is similar to that of the 63.5 mm mesh and covers the size range for the 5 meshes combined. Catches declined from a maximum in the 63.5 mm mesh (56) to 40 and 9 in the 69.9 and 76.2 mm mesh, respectively. Therefore it is unlikely that there was any bias except perhaps against smaller postsmolts.

Fall Movement out of Coastal Reaches

Postsmolts gradually left the nearshore area in late-September. Fishermen in 1982 started collecting postsmolts in mid-August. Their bycatch declined from mid-September and was low in October. The catch declined partly because most commercial fishermen were asked to return no more than 20 salmon each, and they reached this limit early (Table 7). Fishing was initiated later in 1983 and took place over a shorter period (23 September–11 October), but a 68% decline in the catch was observed between the period 29 September–5 October and the period 5–11 October. Finally in 1984, postsmolts came near the coast near the end of August and moved out in mid-September (Table 8) so that no salmon were caught in the period 20 September–20 October.

This movement out of the nearshore zone was associated with decreasing near-surface temperatures in autumn. Temperatures measured near the surface closely followed the mean air temperatures recorded in Sept-Iles (Fig. 5). Since most postsmolts travelled near the surface, mean air temperatures were assumed to reflect prevailing conditions for postsmolts. In 1982, postsmolts were abundant until mean air temperatures declined below 5°C, i.e., in early October. The situation was similar in 3 stations out of 4 in 1983, particularly in the Bay of Matamek River near Sept-Iles and in Rivière Pentecôte, 2 stations closer to our monitoring station. In 1984, this decline in mean air temperature occurred earlier (26 September), but surface temperatures were also lower than air temperatures, and the catch declined (Table 8) as soon as surface temperatures fell below 5°C (mid-September.) Hence, low temperatures were associated with a movement of postsmolts out of the nearshore zone. However, the reverse is not true: results for 1983 and 1984 suggest that postsmolts do not necessarily move towards nearshore zones when prevailing temperature conditions are favorable.

Variations in seasonal abundance are masked by a general decline in salmon abundance near shore from 1982 to 1985. Fishing effort could not be assessed in 1982, but the incidence of postsmolts in coastal herring nets in 1982 was such that it can reasonably be concluded they were more abundant than in 1983, 1984, or 1985. Relative abundance can be assessed for 1983, 1984, and 1985. Baie Trinité and Port Cartier stations were operated in 1983 and 1984 using similar nets at the same locations each year and showed that postsmolts were more abundant in 1983 than in 1984 (Table 9). Finally, a station was monitored near Sept-Iles in 1985 in an area where the best catches were made in 1982, using

TABLE 7.—Time distribution of the commercial bycatch of Atlantic salmon postsmolts in 1982.

Period	Number
10–31 August	210
01–15 September	118
16–30 September	21
01–15 October	24
16–31 October	8

TABLE 8.—Catch of Atlantic salmon postsmolts by period and locality in 1984.

	Locality	
Period	Baie Trinité	Port Cartier
21–24 August	1	4
24–27 August	0	0
27–30 August	0	1
30 August–02 September	0	14
02–05 September	4	8
05–08 September	6	9
08–11 September	0	2
11–14 September	3	16
14–17 September	0	8
17–20 September	0	0
20 September–20 October	0	0

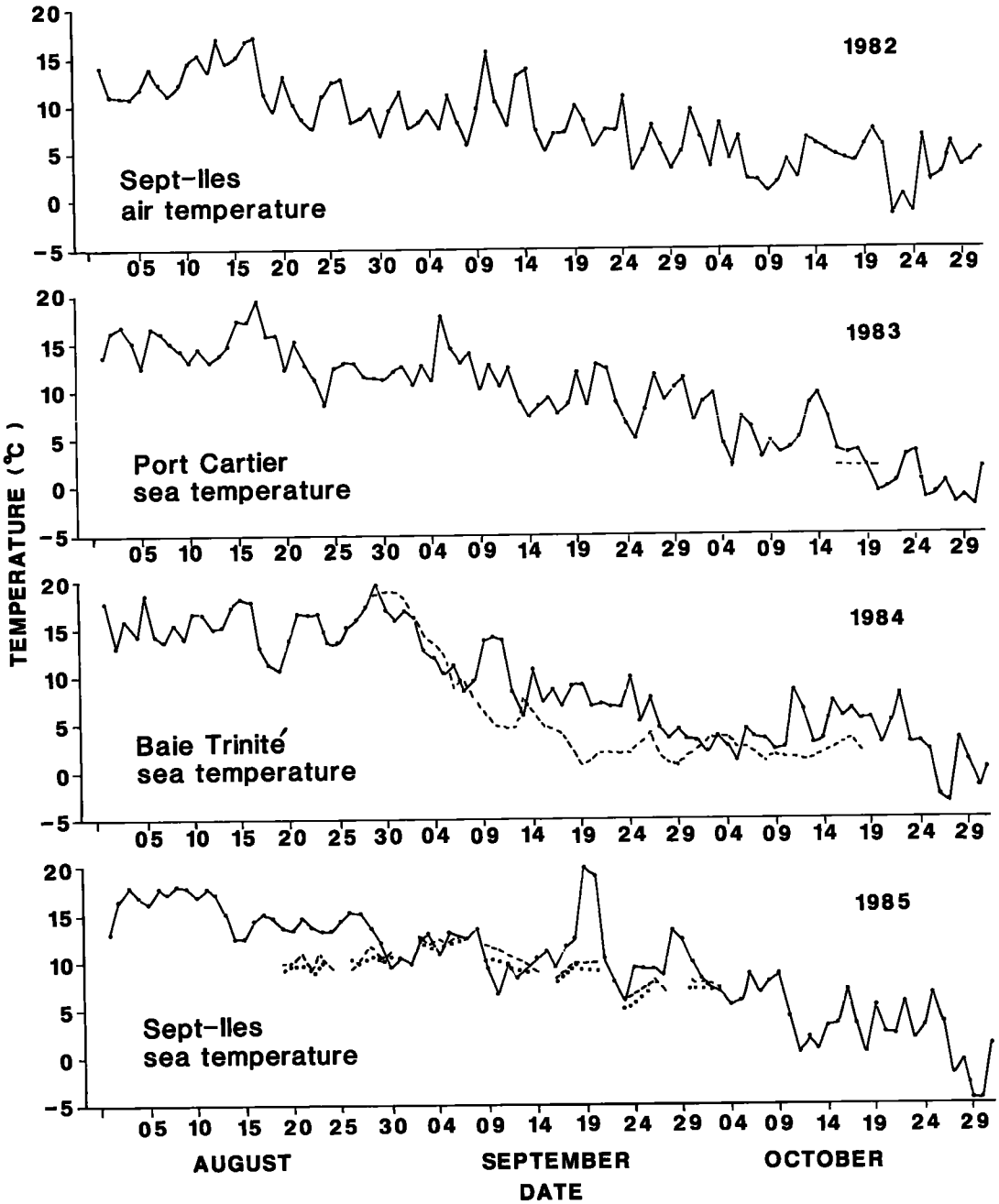

FIGURE 5.—Mean daily air temperature in Sept-Iles (-•-), and mean daily sea temperature at 0.5 m (- - -) in Port Cartier (1983), at 6 m (- - -) in Baie Trinité (1984), and at 0.5 m (- - -) and 6 m (•••••) in Sept-Iles (1985).

TABLE 9.—Relative abundance in terms of catch per unit of effort (CPUE) at 2 stations run in 1983 and 1984 using similar nets at the same sites.

Period	Baie Trinité			Port Cartier		
	Catch	E	CPUE	Catch	E	CPUE
1983						
23 Sept.–11 Oct.	54	38.5	1.4	40	20.0	2.0
1984						
21 Aug.–31 Aug.	1	20.5	0.1	5	32.5	0.2
30 Aug.–17 Sept.	15	54.5	0.3	57	73.0	0.8
17 Sept.–23 Sept.	0	22.0	—	0	17.0	—
23 Sept.–11 Oct.	0	55.5	—	0	45.5	—
11 Oct.–18 Oct.	0	9.5	—	0	21.0	—

[1]CPUE: catch of 1 net in 24 hours.

similar nets to 1983 and 1984. The catch was nearly nonexistent: 5 salmon for 120 unit effort (1 unit effort, is 1 net × 24 hours). Thus, based on limited observations, numbers of salmon near shore in summer and autumn seem to be highly variable from year to year.

DISCUSSION

Postsmolts of Atlantic salmon stay much longer near our coasts than is usually believed. Though early months in the marine environment have been shown to have a marked influence on salmon runs 1 and 2 years later (e.g., Christensen and Larsson 1979; Scarnecchia 1983, 1984), postsmolt biology has been a neglected area of investigation. North American smolts are assumed to migrate rapidly out of the estuaries of their home rivers, to feeding areas located far out in the North Atlantic east of the Grand Bank (Templeman 1968; Reddin 1985) and north to Labrador and Greenland (Saunders 1966; Templeman 1967). They return 1 or 2 years later to spawn in home rivers. This study, and early records, indicate that some postsmolts remain in coastal areas as late as autumn before moving offshore. This was clearly suggested by Comeau (1909) who stated that 0.5–1.5 lb postsmolts were regularly taken in autumn along the north shore of the Gulf of St. Lawrence. Fishermen interviewed in 1982 on the north shore of the Gulf of St. Lawrence, from Pointe-des-Monts to Blanc Sablon, declared incidental catches of postsmolts, mainly in the months of August and September. The majority declared taking postsmolts each year. Smolts were also shown to linger in estuaries of the north shore of the Gulf of St. Lawrence (this study; Power and Shooner 1966; Randall and Power 1979). Huntsman (1939) mentioned their occurrence in autumn in herring nets near the mouth of Gaspé Bay. Fall catches also occurred in New England (Kendall 1935). Recently, smolts released in New England were caught as postsmolts in coastal areas of Canada (Meister 1984). There are stocks in the Bay of Fundy (as the stocks in the Baltic) that do not go on extensive migrations in the North Atlantic (Huntsman 1939; Jessop 1976): postsmolts of these stocks are regularly taken in herring nets in Passamaquoddy Bay and off Grand Manan Island (Elson 1953, 1964; Allen et al. 1972). Hence the presence of postsmolts near shore in autumn (or in summer and autumn) is a characteristic of the marine life of Atlantic salmon in North America. Timing of migration has been described for hatchery-reared smolts released in Sweden (Larsson 1974) and Finland (Jutila and Alapassi 1985). Tags were returned mostly from a distance of less than 10 km between days 0 and 10, 20–50 km between days 10 and 20, and 50–100 km 2 months past their release, in the brackish waters of the Gulf of Bothnia (Jutila and Alapassi 1985).

Behavior of postsmolts is similar to that of 1- and 2-sea-year salmon. Postsmolts in this study occurred mainly near the surface as indicated by their distribution in the nets. LaBar et al. (1978) concluded that smolts migrated near the surface in the Penobscot estuary. Templeman (1967, 1968) also found salmon to occur near the surface in the Northwest Atlantic: 62% occurred in the top 0.6 m and 90% in the top 1.5 m in July and August 1965. Similarly in 1966, most salmon were taken in the top 1.5 m, the number caught decreasing sharply below 0.6 m. Similar observations were made on Baltic salmon (Carlin and Lundin 1967; Christensen 1968). There is less information available on schooling. Postsmolts did not regularly have a clustered distribution in nets, but considering that a net does not retain all the salmon striking it, there were still many instances of salmon moving in schools. Thurow (1968) came to the same conclusion for older salmon in the Baltic. Templeman (1967) presented limited evidence for salmon in the Northwest Atlantic, but reached negative conclusions later (Templeman 1968). Finally there are limited data in the literature concerning the rhythm of activity of salmon in the marine environment. Christensen and Lear (1980) showed that in West Greenland best catches occurred early in the morning (0600–0800), decreased sharply between 0800 and 1000, and were low between 1000 and 1400. The nets were not set between 1400 and

0600. Catches in this study were also low in midday. Either this is a reflection of 2 peaks of activity, dawn and dusk, as is common in salmonids in freshwater, or this is possibly due to salmon avoiding the nets in high light levels. Thus postsmolts and 1- and 2-sea-year salmon appear to have a similar behavior at sea. They move in small schools close to the surface and are possibly more active at dusk and dawn.

Food items in the stomachs of postsmolts changed markedly in summer and indicated a low diversity of prey. This is in contrast to findings reported for salmon in the Northwest Atlantic. Grande Trinité River postsmolts had fed mostly on chironomids and gammarids in late-July. Baltic salmon postsmolts fed mainly on aerial insects though small fish and crustaceans also occurred in the stomachs of postsmolts in the southern Baltic (reviewed by Christensen and Larsson 1979). Jutila and Toivonen (1985) also found aerial insects to be the dominant food items in the stomachs of small postsmolts (<20 cm) in the Gulf of Bothnia (Baltic). They observed that postsmolts were not selective and must have fed near the surface (20 cm surface layer). Postsmolts collected later in the present study relied mainly on small sand lance. Insects and gammarids had been replaced by vertically migrating crustaceans such as *Meganyctiphanes norvegica* (Kulka et al. 1982). Thurow (1968) estimated 25 cm to be the length threshold for piscivorous feeding by Baltic salmon. In the present study, this size was likely reached in the first half of August 1982. This coincides with a major change in stomach contents and a high percentage of stomachs containing no food. The data on postsmolts in July are too limited to suggest that sand lance abundance could limit the early success of postsmolts at sea, but potential relationships in late summer should be tested as was done for capelin by Reddin and Carscadden (1981). Data on 1- and 2-sea-year salmon indicate they will readily feed on a diversity of prey items, main items including Arctic squid, *Gonatus fabricii*; paralepids, *Paralepis coregonoides*; and lantern fishes (*Lampenyctus* sp., *Notoscopelus* sp.) (Templeman 1967, 1968; Lear 1980). Sand lance and capelin are dominant items in West Greenland and on the coast of Newfoundland (Lear 1972, 1980), and on the Grand Bank (Reddin 1985). Reddin (1985) observed major changes in stomach contents between salmon on the Grand Bank (sand lance and capelin) and east of the Grand Bank (Bathylagidae, *Paralepis* sp., and crustaceans), emphasizing that salmon are not selective predators.

The rate of increase in mean length averaged 1.65 mm/day in the Gulf of St. Lawrence over the summer period in 1982 and 1983. This value is based on the hypothesis that smolts migrated to estuaries in mid-June. Smolt migration took place in the first half of June in Restigouche River in the southern Gulf of St. Lawrence (Peppar 1982) and in the second half of June in Grande Trinité River in the northern Gulf of St. Lawrence (Caron 1984). Downstream migration of smolts peaked at various dates in June in Western Arm Brook in western Newfoundland (Chadwick 1981). The calculated rate of increase is also based on a mean back-calculated smolt length of 135 mm. Length at smoltification averaged 125–130 mm in Grande Trinité River (mean and SD: 127.5 ± 12.3, $n = 88$, in 1981; 125.8 ± 10.9, $n = 92$, in 1982; see also Caron 1984). Matamek River and Moisie River smolts measured 125–150 mm (Schiefer 1972). They measured 150 mm in Little Codroy River (Murray 1968) and 174 mm in Western Arm Brook (Chadwick 1981). There are no data in the literature concerning the rate of increase in size of smolts and postsmolts in the marine environment. Postsmolts in the Bay of Fundy reached a mean length of 296 mm in mid-August 1952 (Allen et al. 1972), some 3 cm more than postsmolts in this study: 265 mm and 306 mm on 1 September and 30 September. However the high value of the power exponent of the length-weight relationship as compared with salmon in Newfoundland and Labrador (Lear 1973) indicates postsmolts were not in poor condition. There was possibly a decline in the rate of increase in length in mid-summer as suggested by the large proportion of scales showing a summer check (false-annulus) in 1983. This occurred 10 circuli from the smolt check in mid-summer in postsmolts 20–22 cm in length, i.e., prior to this study period, and may have been produced as a response to a shortage of prey or to deteriorating environmental conditions. Elson (1953) also noticed the frequent occurrence of a slowing of growth 6–10 circuli out from the last parr annulus. The percentage of occurrence of the check varied between locations (1982) and between years (1982 < 1983 < 1984). Therefore it is not likely to be a response to a change in postsmolt biology such as a scheduled shift in prey selection. However, the summer check can be thought of as a potential tool for stock discrimination. Some 26–32 circuli are formed before the first sea an-

nulus is formed (Lear and Misra 1978) at a length of 46–50 cm in the first half of April (Munro 1970).

Presence of postsmolts near shore in late summer in the northern Gulf of St. Lawrence, as reported in this study, and presumably their late movement out of the Gulf of St. Lawrence indicate that the directional nature of the migration should be reconsidered. There are some smolts that do not head towards the high seas as soon as they reach the estuaries. They seem to roam nearby unless prevailing conditions are not favorable. Temperature can be hypothesized as triggering the late movement of postsmolts out of the northern Gulf of St. Lawrence. Saunders (1986) reviewed the thermal biology of Atlantic salmon and suggested the thermal range for salmon in the sea is lower than for juvenile salmon in freshwater. Salmon occur mainly at temperatures ranging from 4° to 8°C in the Northwest Atlantic (Templeman 1968; May 1973; Reddin 1985). Postsmolt movements out of the nearshore area took place in a short period as temperature was decreasing, between mid-September and mid-October. Postsmolts were more abundant in 1982 and 1983 as mean air temperature ranged between 4° and 10°C in early autumn. In 1984, sea temperature decreased rapidly from more than 15°C in late-August down to 2°C in mid-September; postsmolts vanished from the nearshore area as temperature declined below 4°C. However in 1985, they did not come near the coast though sea temperature ranged between 8° and 12°C. Saunders et al. (1975) reported the lethal temperature of salmon in seawater to be −0.7°C. This precludes the possibility of salmon overwintering in the Gulf of St. Lawrence unless they return to freshwater, as do some salmon in the Koksoak River (Côté et al. 1984; Robitaille et al. 1984a, b), or move down to midwater, a behavior described for salmon in the Baltic in response to high temperatures (>12°C) at the surface (Alm 1958). Comeau (1909) reported postsmolts found in the stomach of seals off Pointe-des-Monts in January and February. Low sea temperature has been hypothesized as limiting the passage of Koksoak River smolts (Ungava Bay) to West Greenland in some years, thereby resulting in an estuarine population (Power 1969, 1981). This situation might also be hypothesized to occur in the Gulf of St. Lawrence. For instance in 1983, mean air temperature, not to mention minimal temperature, decreased from 4° to 0°C and less in a short period near the end of October. Masses of seawater carried by gyres east and west of Anticosti Island, and presenting momentarily favorable conditions, can get surrounded by masses of seawater at lower temperature. Should salmon rely on temperature as a cue for their movement out of the Gulf of St. Lawrence, then late migrants could not escape as conditions deteriorate.

The origin of postsmolts collected in this study is not known. They may be a particular subgroup of some north shore stocks. Postsmolts in this study smoltified earlier and at a smaller size than stocks in northern Newfoundland (Chadwick 1981). However, their origin cannot be determined based on smolt length or smolt age distributions. For instance, there is a general tendency for increasing smolt age with latitude, but there is much variability in the data at latitudes below 52°. Data for salmon stocks in rivers near 50° latitude range from 3 to 4 years (Power 1981). Furthermore, postsmolts in this study had an age distribution similar to that of salmon in the Port-aux-Basques (Newfoundland) drift net fishery. Port-aux-Basques salmon migrated to rivers all around the Gulf of St. Lawrence (Belding and Préfontaine 1938).

Postsmolts in this study may also be from a particular subgroup of individuals, such as late-migrant smolts. Power and Shooner (1966) and Randall and Power (1979) observed remnants of the smolt migration feeding in river estuaries on the north shore of the Gulf of St. Lawrence in July and August. Furthermore coho salmon released in mid- to late-summer did not leave the general area of release (Mahnken and Joyner 1973).

Since grilse are known not to migrate as far as 2- and 3-sea-year salmon in the Northwest Atlantic (Ruggles and Ritter 1980), postsmolts in this study can be thought of as potential grilse. However, the only indication in that direction that we have is the observation that some males having a summer check on their scales in 1982 had a higher gonadosomatic index than males having no summer check on their scales (0.042 and 0.025% respectively). However, this is based on a small number of postsmolts as few salmon exhibited a summer check in 1982 and, unfortunately, no gonads were preserved in 1983–85. There are some stocks maturing mainly as grilse among the north shore stocks, but grilse are nearly exclusively males in these stocks (Schiefer 1972; Caron 1984). Postsmolts in this study were 62% females. Female grilse are common in Newfoundland (Chadwick 1981; Power 1981). There are no published data on Anticosti stocks. Poten-

tial grilse have been reported from the Grand Bank in offshore fisheries in the Northwest Atlantic (Reddin 1985), and it has been suggested that stocks maturing as grilse in the Bay of Fundy may not leave the general area throughout their entire marine life (Jessop 1976).

Knowledge on the marine biology of Atlantic salmon postsmolts has been a neglected area of research. Their continual presence in sea surface waters could prove to be extremely valuable in forecasting salmon movements and production (Chadwick 1982; Scarnecchia 1984). Potential studies include mortality rates in the period of transition (July) and the relationship between low temperatures (3°–4°C) and postsmolt migration out of the Gulf of St. Lawrence. Biological data in general are needed to be included in models forecasting salmon runs in the North Atlantic.

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SIZE AND DIET OF JUVENILE PACIFIC SALMON DURING SEAWARD MIGRATION THROUGH A SMALL ESTUARY IN SOUTHEASTERN ALASKA

MICHAEL L. MURPHY, JOHN F. THEDINGA, AND K V. KOSKI[1]

ABSTRACT

To assess competition and predation among juvenile Pacific salmon (*Oncorhynchus* spp.) migrating through the estuary of Porcupine Creek, a small stream in southeastern Alaska, their size and diet were determined in 1979 and 1981. Mean fork length (FL) during May and June increased from 32 to 73 mm (1.5 mm/day) for pink salmon, *O. gorbuscha*; from 39 to 51 mm (0.4 mm/day) for chum salmon, *O. keta*; and during June and July, from 99 to 165 mm (1.6 mm/day) for coho salmon, *O. kisutch*. Prey, in order of importance, included larval fish (mostly Gadidae), larval molluscs (Mesogastropoda), and calanoid copepods for pink salmon; larval molluscs, larvaceans, and hyperiid amphipods for chum salmon; and fish (*Clupea harengus pallasi, Ammodytes hexapterus*, and Gadidae), insects, and larval decapods (Brachyrhyncha) for coho salmon. No pink or chum salmon were found in the coho salmon stomachs. Prey size for pink and chum salmon was similar (median, 0.4 mm long for both species), and much smaller than that of coho salmon (median, 2.3 mm). Diet overlap was greater between pink and chum salmon than between either species and coho salmon. Pink salmon, however, ate almost exclusively (95%) pelagic prey, whereas chum salmon ate both pelagic (74%) and epibenthic (26%) prey. Rapid early growth and differences in diet probably help minimize predation and competition among salmon during seaward migration.

The early marine life stage of juvenile Pacific salmon (*Oncorhynchus* spp.), during transition from freshwater to seawater, is important in determining brood-year survival and subsequent adult returns (Manzer and Shepard 1962; Parker 1968); their survival rate is lowest during this time (Parker 1968; Bax 1983). Salmon often school in large concentrations in estuaries as they migrate seaward, and are more likely to deplete food supplies and compete for food than after they disperse to the sea (Bailey et al. 1975; Feller and Kaczynski 1975). Survival depends on size (Parker 1971; Healey 1982), and competition for food can depress early growth (Peterman 1984) and prolong vulnerability to predators (Taylor 1977; Walters et al. 1978). Size and diet of juvenile salmon in an estuary, therefore, determine the potential for predation and competition and can greatly affect survival.

As salmon aquaculture expands and more juvenile salmon are released into estuaries, competition and predation among salmon may increase (Johnson 1974). To optimize hatchery production and avoid adversely affecting wild stocks, an understanding is needed of how different stocks of salmon interact in estuaries. This paper compares size and diet of juvenile pink, *O. gorbuscha*; chum, *O. keta*; and coho, *O. kisutch*, salmon to assess potential predation and competition between the species during their seaward migration through the estuary of a small, pristine stream.

STUDY AREA

This study was conducted in the estuary of Porcupine Creek, the only salmon stream flowing into Steamer Bay in southeastern Alaska (Fig. 1). The estuary (about 5.5 km long) consists of a 1.5 km stream reach that is periodically inundated by tides, and a 4 km series of three estuarine basins. At low tide, the inner and middle basins are small (2 and 7 ha, respectively) and shallow (14 and 16 m, respectively) compared with the outer basin (120 ha and 42 m deep). The littoral zone ranges from low-gradient mudflats to steep cobble. Bottoms of the basins are level and composed of shell, gravel, and mud.

During low tide, the inner and middle basins are partially isolated from the outer basin and the main part of Steamer Bay by tidal rapids 1–3 m deep. Salinity is lower in the inner and middle

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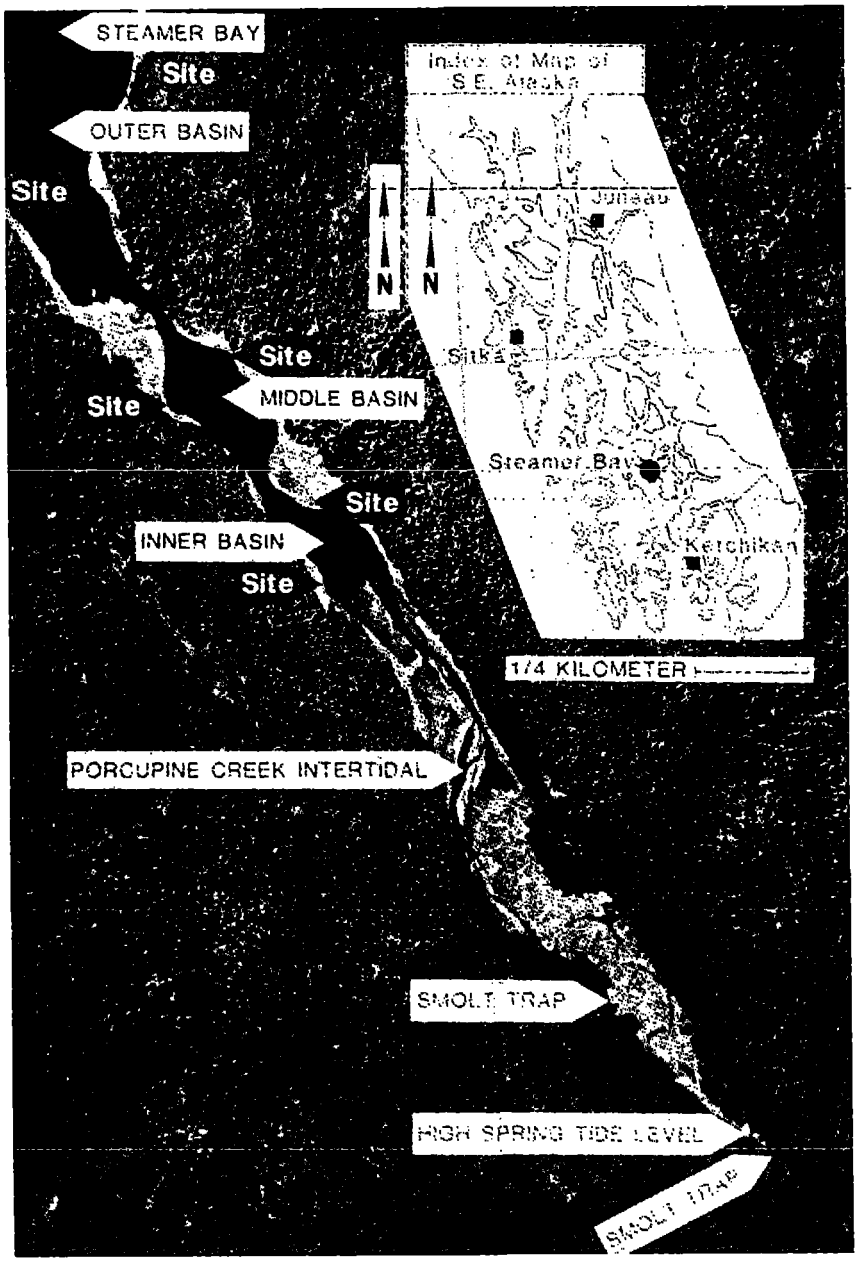

FIGURE 1.—Aerial photo of study site in the inner part of Steamer Bay, southeastern Alaska, showing the Porcupine Creek estuary at low tide and location of smolt traps used by Thedinga (1985).

basins (24–29‰) than in the outer basin (28–30‰), but temperature does not differ between basins in spring and summer (11°–13°C from May to September 1981). Heavy tidal flushing, particularly during spring tides, results in a diverse community within the estuary; e.g., eel grass, *Zostera*; Dungeness crabs, *Cancer magister*; bull kelp, *Nereocystis*; and rock scallop, *Hinnetes*. A detailed description of the study area is in Merrell and Koski (1978) and Koski (1984).

Porcupine Creek, upstream of tidal influence, is 4.5 km long and has an average discharge of

about 0.5 m^3/second. Its watershed is forested by mature western hemlock, *Tsuga heterophylla*, and Sitka spruce, *Picea sitchensis*. Annually, 5,000–75,000 adult pink salmon and 200–4,000 chum salmon spawn in the creek from late July to October, and 250–600 adult coho salmon spawn from late September to November (Koski 1984). Pink and chum salmon fry typically migrate from Porcupine Creek from late March to mid-May (Koski[2]). Coho salmon smolts migrate from late April to early June, but over 90% usually migrate in late May (Thedinga 1985).

METHODS

Six stations, one each on the east and west sides of the three basins (Fig. 1) were sampled by a beach seine 37 m long, with 1.6 cm stretch mesh on the wings, and a central bag of 6 mm stretch mesh. The seine tapered from 2 m deep at the central bag to 1 m deep at each end. In 1979, only one station in each basin was seined about every 4 days from 16 May to 12 June. In 1981, all six stations were seined biweekly from 26 May to 7 July and monthly thereafter through 11 November. Seines were set parallel to and about 40 m from shore by a skiff, and retrieved from shore. Setting and retrieval were accomplished within 10 minutes.

All fish caught were identified and counted. Fork lengths (FL) were measured to the nearest millimeter from a random sample of ≤25 salmon per species, station, and sampling period. Stomach contents were collected only in 1981 from ≤10 salmon per species and station in May, June, and July. Contents were collected from anesthetized fish by flushing the stomach with water from a syringe (Meehan and Miller 1978; Koski and Kirchhofer 1984) and preserved in 5% formaldehyde. Prey were later identified, counted, measured, and weighed.

For diet analysis, the index of relative importance (IRI) was calculated, where

$$\text{IRI} = (\%\ \text{number} + \%\ \text{weight})\ (\%\ \text{frequency of occurrence})$$

(Pinkas et al. 1971). Diet overlap between salmon species was calculated (McCabe et al. 1983):

$$C = \frac{2\sum_{i=1}^{s} X_i Y_i}{\left(\sum_{i=1}^{s} X_i^2 + \sum_{i=1}^{s} Y_i^2\right)}$$

where C = overlap coefficient and X_i and Y_i are proportions of the total diet of salmon species X and Y, respectively, contributed by prey taxon i of s prey taxa. Diet overlap was calculated separately for proportions based on prey number and weight. Prey were also classified as epibenthic or pelagic to assess overlap in foraging mode (Feller and Kaczynski 1975). Epibenthic prey were polychaetes, gammarid amphipods, harpacticoid copepods, barnacle cyprids, and cumaceans. Pelagic prey were calanoid copepods, euphausiids, barnacle nauplii, cladocerans, larvaceans, larval decapods (Brachyrhyncha), hyperiid amphipods, and fish (eggs, larvae, and juveniles).

RESULTS

Size

In May 1979, pink salmon were the size of newly emergent fry, about 32 mm FL (Fig. 2). Average length increased 1.5 mm/day, to 73 mm on 12 June 1979. In 1981, pink salmon averaged 73 mm FL in late May and early June. Changes in average FL in 1981 could not be calculated because most migration occurred before sampling began.

Average FL of chum salmon increased slower than that of pink salmon. Mean FL of chum salmon increased 0.4 mm/day in both years, from 39 mm to 51 mm in 1979, and from 60 mm to 78 mm in 1981 (Fig. 2). Chum salmon averaged about 10 mm FL longer in 1981 than in the same period in 1979. Chum salmon were not found in the estuary after early July, except for two fry caught in the outer basin in November.

Average FL of coho salmon was nearly constant, between 85 and 110 mm, throughout May and early June in both 1979 and 1981 (Fig. 2). Average FL of coho salmon in the estuary during this period was influenced by an influx of Porcupine Creek migrants, which averaged between 75 and 96 mm FL (Thedinga 1985). After the migration from Porcupine Creek in 1981 (≈9 June), average FL increased 1.6 mm/day to 165 mm by 20 July. Average FL then decreased to 85 mm in

[2]K. V. Koski, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. October 1985.

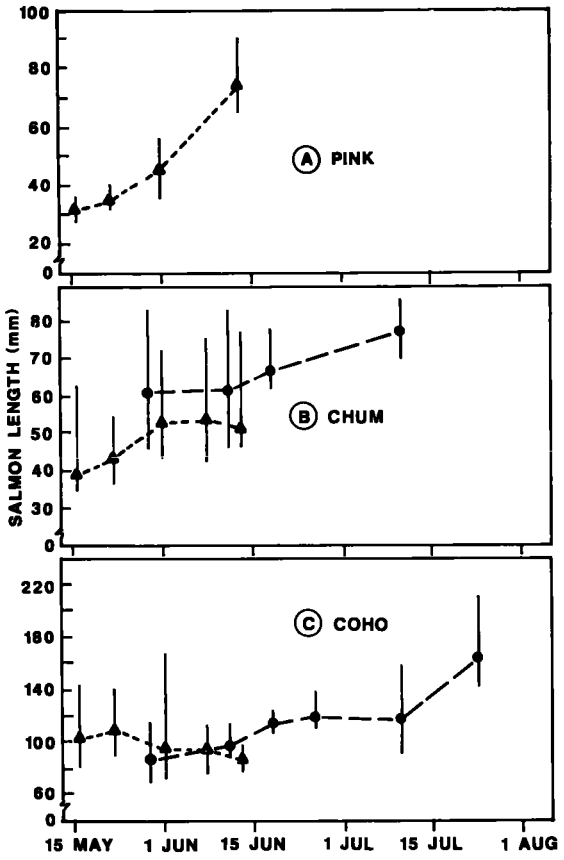

FIGURE 2.—Length of salmon in 1979 and 1981. Data shown are means and ranges for pooled samples from all stations on each sampling date. Data for pink salmon in 1981 are omitted because of small sample sizes. (▲ = 1979, ● = 1981.)

August and 106 mm in September, after most smolts had left and a few new smolts entered the estuary.

Diet

A wide variety of prey was eaten by the three salmon species, but usually only one or two prey taxa dominated the diet (Table 1). Pink salmon ate mostly larval molluscs (Mesogastropoda) and larval fish (mostly Gadidae) in May, and calanoid copepods in June. Chum salmon ate mostly larval molluscs in May; larval molluscs, larvaceans, and cladocerans in June; and hyperiid amphipods and larval decapods in July. Coho salmon ate mostly fish and insects in May and June, and fish and larval decapods in July. The identifiable fish prey of coho salmon consisted of 53% Pacific herring, *Clupea harengus pallasi*; 45% cod (Gadidae); and 2% Pacific sand lance, *Ammodytes hexapterus*. No identifiable pink or chum salmon were in the coho stomachs. Catch of coho, but not that of the other salmon, was significantly correlated ($r = 0.46$, $P < 0.001$) with aggregate catch of herring, sand lance, and cod, indicating that coho salmon congregated near prey schools.

Diet overlap was higher between pink and chum salmon than between either species and coho salmon (Table 2). Diet overlap between pink and chum salmon was especially high in May when both species ate large numbers of larval molluscs. If based on prey weight, diet overlap between pink and coho salmon was negligible. If based on prey number, however, overlap was >50% in June when both pink and coho salmon ate large numbers of calanoid copepods. Diet overlap between chum and coho salmon was consistently low, especially when based on prey weight.

Of the 12 most important prey taxa in May and June, when all 3 salmon species were present in the estuary, only 4 differed significantly ($P < 0.05$) in mean number per stomach between pink and chum salmon, whereas 9–10 differed significantly between the two species and coho salmon (Table 3). Compared with pink salmon, chum salmon ate more harpacticoid copepods, cladocerans, and insects. Coho salmon ate fewer small plankton and more fish than did the other salmon species. Coho salmon averaged fewer than 20 total prey items, compared to more than 100 in pink salmon and 200 in chum salmon.

Coho salmon ate larger prey than did the other salmon (Fig. 3). Median prey length for coho salmon was 2.3 mm, compared with 0.4 mm for pink and chum salmon. Coho salmon generally selected larger individuals of each prey taxon—particularly larger calanoid copepods, gammarid amphipods, euphausiids, and larval decapods—than did pink and chum salmon (Table 4). Of fish prey, coho salmon ate mostly juveniles, whereas pink and chum salmon ate mostly eggs and larvae.

As they grew larger, all three salmon species selected larger prey. Numbers of hyperiid amphipods, euphausiids, and fish larvae—all relatively large prey—were positively correlated with FL of pink or chum salmon, whereas numbers of cladocerans and larvaceans—both relatively small prey—were negatively correlated with chum salmon FL (Table 5). Numbers of calanoid copepods and fish were positively correlated with coho salmon FL, whereas the number

TABLE 1.—Stomach contents of juvenile salmon in Porcupine Creek estuary, 26 May–7 July 1981. %*N* is percent by number, %W is percent by wet weight, %FO is percent frequency of occurrence of fish with prey item *i*, and %IRI is percent of total sum of IRI for all prey taxa. IRI = (%*N* + %*W*)%FO. Taxa are omitted if %IRI is ≤3 for all salmon species.

Prey taxon	Pink salmon				Chum salmon				Coho salmon			
	%*N*	%*W*	%FO	%IRI	%*N*	%*W*	%FO	%IRI	%*N*	%*W*	%FO	%IRI
26–29 May 1981												
Mollusc larvae	47	2	71	28	59	36	100	60	2	0	4	0
Calanoida	12	2	57	7	5	4	71	5	0	0	4	0
Harpacticoida	1	0	29	0	11	9	90	12	17	1	18	3
Cladocera	1	0	43	1	14	5	77	10	0	0	4	0
Cumacea	0	0	0	0	2	9	32	3	16	1	41	6
Euphausiacea	11	2	71	8	0	2	42	1	0	0	0	0
Decapod larvae												
Shrimp	9	5	71	8	0	1	13	0	0	0	0	0
Crabs	8	2	60	4	3	3	60	2	2	0	12	0
Fish eggs												
and larvae	8	86	57	44	0	21	13	2	1	6	4	0
Fish	0	0	0	0	0	0	0	0	22	62	48	38
Insects[1]	1	0	29	0	1	5	52	2	29	23	100	47
Total	98	99		100	95	95		97	89	93		94
(Number of stomachs)			(7)				(31)				(27)	
9–10 June 1981												
Mollusc larvae	9	5	100	8	24	16	73	23	0	0	7	0
Calanoida	47	52	100	58	5	5	65	5	22	0	43	9
Harpacticoida	3	5	25	1	4	4	65	4	0	0	7	0
Cladocera	13	7	75	9	19	8	81	17	1	0	23	0
Decapod larvae												
Shrimp	1	1	75	1	0	1	20	0	0	0	0	0
Crabs	4	11	100	5	7	12	100	8	19	0	21	4
Larvacea,												
Oikopleura	9	5	100	8	20	13	85	23	7	0	14	1
Fish eggs												
and larvae	6	5	100	6	11	12	35	6	0	0	0	0
Fish juveniles	0	0	0	0	0	0	0	0	10	94	71	70
Insects[1]	0	1	50	0	3	10	75	8	28	2	50	14
Total	92	92		96	93	91		94	87	96		98
(Number of stomachs)			(4)				(26)				(14)	
7 July 1981												
Calanoida	—	—	—	—	4	1	43	3	16	0	24	5
Hyperiidea	—	—	—	—	12	30	88	45	4	0	29	2
Decapod larvae												
Shrimp	—	—	—	—	61	40	14	18	1	0	6	0
Crabs	—	—	—	—	3	10	86	9	55	5	53	25
Fish eggs												
and larvae	—	—	—	—	0	3	57	2	0	0	0	0
Fish juveniles	—	—	—	—	0	0	0	0	9	94	50	65
Insects[1]	—	—	—	—	6	4	100	14	5	0	24	2
Total	—	—	—	—	86	88		91	90	99		99
(Number of stomachs)			(0)				(7)				(17)	

[1]Mostly adult Diptera.

of insects was negatively correlated. As a consequence of the selection of larger prey as the salmon grew, total prey weight increased with salmon FL, whereas total prey number did not (Table 5). Although pink and chum salmon ate prey of similar size, they foraged differently (Fig. 4). Pink salmon consumed about 95% pelagic prey; chum salmon, only 74%. Individual taxa changed, but the importance of pelagic prey did not change significantly between sampling periods, estuary basins, or salmon FL classes.

Diet of coho salmon, on the other hand, varied widely depending on salmon FL, date, and location (Fig. 4). Pelagic prey increased from 1% of total prey for coho salmon <80 mm FL to 80% for those >100 mm FL. Coho salmon ate fewer pelagic prey in May, when most coho were in the inner basin and feeding mainly on insects, than in July when most were in the outer basin and feeding mainly on fish (Table 1). Analysis of variance, however, showed that differences between basins and sampling periods were not significant

TABLE 2.—Diet overlap (McCabe et al. 1983) based on number (n) and weight (W) of prey by sampling period for juvenile salmon in Porcupine Creek estuary, 26 May–7 July 1981. The number of stomach samples is in Table 1.

Sampling period	Pink vs. chum		Pink vs. coho		Chum vs. coho	
	n	W	n	W	n	W
26–29 May	0.87	0.40	0.07	0.09	0.13	0.08
9–10 June	0.47	0.38	0.54	0.00	0.29	0.00
7 July	—	—	—	—	0.10	0.01

TABLE 3.—Comparison of mean number of the 12 most important prey and total of all prey per salmon stomach from Porcupine Creek estuary, 26 May–10 June 1981. Means followed by the same letter are not significantly different (Kruskal-Wallis analysis of variance, $P>0.05$) compared within a row and across columns. The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	28 a	86 a	0 b
Barnacle larvae	4 a	5 a	0 b
Calanoida	40 a	12 b	0 b
Harpacticoida	2 a	19 b	3 a
Cladocera	10 a	37 b	0 c
Cumacea	0 a	5 a	2 a
Euphausiacea	5 a	1 a	0 b
Decapod larvae	11 a	12 a	0 b
Larvacea	6 a	20 a	0 b
Fish eggs and larvae	3 a	11 a	0 b
Fish	0 a	0 a	4 b
Insects	0 a	4 b	6 b
Total	115 a	216 a	19 b

TABLE 4.—Mean length (mm) of prey items in salmon stomachs from Porcupine Creek estuary, 26 May–7 July 1981. Mean prey length within prey taxa was significantly greater for coho salmon than for pink or chum salmon (sign test, $n=12$ means, $P=0.03$ and $P=0.003$, for coho salmon vs. pink and chum salmon, respectively). The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	0.5	0.5	0.4
Barnacle larvae	0.4	0.7	0.4
Calanoida	1.2	1.2	4.8
Harpacticoida	1.3	1.1	1.3
Cladocera	0.6	0.6	0.7
Cumacea	2.4	2.5	2.8
Hyperiidea	3.3	2.4	3.0
Gammaridea	1.5	1.8	5.2
Euphausiacea	3.5	3.0	18.0
Decapod larvae	2.8	2.0	3.5
Larvacea	0.8	0.9	—[1]
Fish, all life stages	2.0	1.2	23.9
Insects	2.8	2.2	3.5

[1]None present.

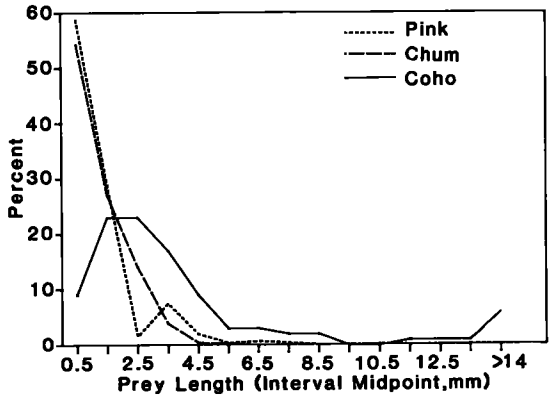

FIGURE 3.—Relative frequencies of length of prey eaten by pink, chum, and coho salmon in the Porcupine Creek estuary in 1981. Total prey measured were 687 in 11 pink, 5,634 in 63 chum, and 1,179 in 53 coho salmon.

TABLE 5.—Spearman rank correlations between number of prey items and fork length of juvenile salmon. Because of the large number of correlations tested, significance levels were adjusted by multiplying the probability P by the number of tests for each salmon species. The number of stomach samples is in Table 1.

Prey item	Pink salmon	Chum salmon	Coho salmon
Mollusc larvae	−0.32	0.05	−0.18
Barnacle larvae	−0.36	−0.02	0.22
Calanoida	−0.51	0.10	0.33*
Harpacticoida	−0.30	−0.03	−0.19
Cladocera	−0.06	−0.34*	−0.04
Cumacea	−0.20	0.04	−0.28
Hyperiidea	−0.35	−0.37*	0.19
Euphausiacea	0.84*	0.36*	0.15
Decapod larvae	0.43	−0.19	0.25
Larvacea	−0.36	−0.50*	—[1]
Fish eggs	−0.33	−0.18	—[1]
Fish larvae and juveniles	0.86*	−0.04	0.36*
Insects	0.61	−0.11	−0.71**
Total prey number	−0.40	−0.04	−0.09
Total prey weight	0.85*	0.35*	0.66**

[1]None present in any stomachs.
*Adjusted probability $P < 0.05$.
**Adjusted probability $P < 0.01$.

after adjusting for differences in coho salmon FL (Table 6). Thus, changes in diet were mainly related to increasing size of coho salmon as they migrated through the estuary.

DISCUSSION

Both size and diet can affect predation and competition among juvenile salmon in an estuary. A

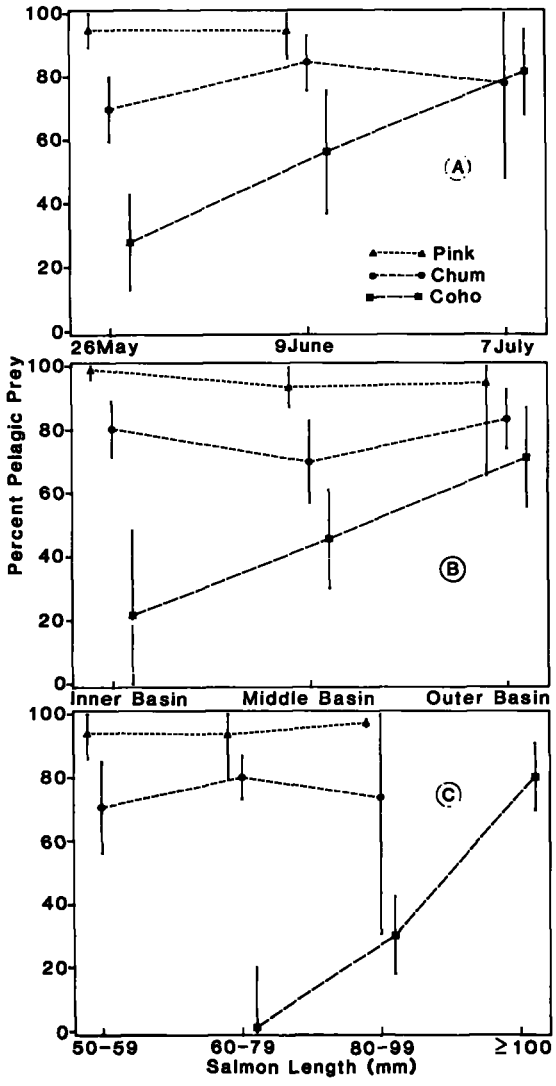

FIGURE 4.—Number of pelagic prey as percent of total prey eaten by individual salmon compared between sampling periods (A), estuary basins (B), and salmon fork length classes (C) in the Porcupine Creek estuary in 1981. Symbols are means; bars are ±2 SE of the means. Symbols in *B* and *C* are the same as in *A*. Pelagic prey are defined in the text.

salmon's size mainly influences its vulnerability to predators, whereas its diet determines potential competition for food. Size and diet, however, are not independent. Salmon change their diet as they grow, which helps relieve competition between salmon of different size, and a poor diet slows their growth, which prolongs vulnerability to predation.

TABLE 6.—Analysis of variance of percentage pelagic prey of coho salmon, with sampling period and estuary basin as factors and salmon fork length as covariate. Factors, covariate, and interactions were adjusted simultaneously before assessing significant (Kim and Kohout 1975).

Source of variation	df	Mean square	*F*	*P*
Length	1	8,458	9.4	0.004
Sampling period	2	1,580	1.8	0.184
Basin	2	654	0.7	0.489
Residual	47	900	—	—
Total	52	1,519	—	—

Because of similar diets, pink and chum salmon are potential competitors. Although diets of pink and chum salmon in the Porcupine Creek estuary were similar in prey size and some prey taxa, however, pink salmon fed almost solely on pelagic prey , whereas chum salmon foraged both pelagically and epibenthically; such differences may help reduce competition. Competition probably also was reduced because, as the salmon grew larger, they switched to larger prey. Coho salmon probably did not compete for food with the other two species because the coho fed on larger, different prey.

Rapid early growth of salmon is important in reducing vulnerability to predators (Parker 1971; Taylor 1977). For example, hatchery pink salmon fry raised for 60 days (to 40 mm FL) before release into an estuary in southeastern Alaska survived 68% better at sea than did fry released immediately after emergence (Martin et al. 1981). Marine survival also is higher for year classes of larger (9–11 cm FL) than for smaller (6–8 cm FL) sockeye salmon, *O. nerka*, smolts (Foerster 1954). Coho salmon smolts from Porcupine Creek in 1978 averaged 99 mm FL and their survival was twice that of the 1979 smolts, which averaged only 91 mm FL (Thedinga 1985). Smolt size and migration timing, however, interact complexly to influence marine survival of coho salmon (Bilton 1978).

Growth of juvenile salmon in estuaries usually is inferred from changes in mean size (LeBrasseur and Parker 1964; Healey 1978), but these estimates are subject to bias. In this study, changes in mean size of fish in the catches on successive dates could underestimate real growth for two reasons: 1) small individuals may have migrated continuously into the estuary from

freshwater and 2) larger individuals may have migrated continuously from the estuary to the sea. Conversely, growth could be overestimated if predators of salmon selected small individuals (Parker 1971). In addition, although the inner and middle basins are semiisolated from adjacent marine waters during low tide, juvenile salmon from adjacent waters could easily enter the estuary, especially the outer basin, during flood tide and mix with salmon from Porcupine Creek.

Estimates of salmon growth in estuaries and nearshore marine waters are variable, but generally range between 1 and 2 mm/day. LeBrasseur and Parker (1964) estimated pink salmon growth to be 0.9 mm/day during the first 30 days at sea, and Healey (1978) estimated pink salmon growth during summer to be 1.0 mm/day; our estimate was 1.5 mm/day. Our estimate for chum salmon at 0.4 mm/day was considerably less than that of Healey (1978) at 1.5 mm/day, also based on change in mean length; however, our estimate for coho salmon of 1.6 mm/day was similar to that of Healey (1978) at 1.2 mm/day. Summer growth back-calculated from scales of salmon from the Sea of Okhotsk was about 1.6 mm/day for pink and chum salmon (Birman 1969).

Because of their initial small size, pink and chum salmon particularly are vulnerable to predators including juvenile coho salmon (Parker 1971). Several authors have suggested that a major share of pink salmon mortality in the first weeks at sea results from juvenile coho salmon predation (Parker 1971; Kaczynski et al. 1973; Hargreaves and LeBrasseur 1985), but such predation has not been found in field collections. Parker (1971) demonstrated predation by juvenile coho salmon on pink salmon fry in the laboratory, and juvenile coho salmon are known predators of salmon fry in freshwater (Hunter 1959; Koski and Kirchhofer 1984). However, we have not found any published data that show predation by juvenile coho salmon on other salmon in estuaries or marine waters. Predation by juvenile coho salmon on pink salmon fry migrating from freshwater does occur in the tidal-influenced reach of Porcupine Creek (Koski and Kirchhofer 1984), but such predation apparently does not extend into the estuarine basins. Many fishes have been identified as predators of pink and chum salmon in estuaries, including Pacific herring (Thorsteinson 1960), sea-run cutthroat trout, *Salmo clarki*; cod, *Gadus macrocephalus*; and sculpin, *Leptocottus armatus*, (Bax et al. 1977). We speculate that predation by coho salmon on salmon fry may occur only under circumstances in which the coho salmon are combined with small fry as they migrate from freshwater.

The period of vulnerability of pink and chum salmon fry to predation by juvenile coho salmon is probably relatively short. Within the first 3 weeks after entering the estuary, pink salmon fry can grow larger than the prey fish of juvenile coho salmon. In the laboratory, juvenile coho salmon ate the smallest pink salmon available and did not eat any larger than about 50 mm FL (Parker 1971), which coincides with the largest fish eaten by coho salmon in our study. At a growth of 1 mm/day, pink salmon entering the estuary at 32 mm FL will outgrow predation by coho salmon smolts in 18 days. In Porcupine Creek, most pink and chum salmon migrated from the stream several weeks before coho salmon, which enables them to grow large enough to avoid predation by coho salmon in the estuary. Thus, early migration and rapid growth of pink and chum salmon fry probably are important in reducing predation by coho salmon.

In the Porcupine Creek estuary, competition and predation probably were slight. Competition for food was minimal, as evidenced by the rapid salmon growth, because of differences in prey and foraging mode and because regular tidal flushing probably replenished food supplies, as in Traitors Cove, AK (Bailey et al. 1975). Natural stocking levels in the estuary also probably were below thresholds where competition for food would depress survival. Predation by coho salmon on pink and chum salmon was avoided because the pink and chum salmon migrated earlier than coho salmon and rapidly grew too large for the coho to handle. Thus, in this natural system, competition and predation probably were unimportant because of moderate stocking levels, rapid growth, and differences in diet and timing of migrations. In systems with hatchery inputs, however, stocking levels would probably be higher and salmon size and timing of migrations different than in natural systems, which could increase competition and predation.

Stocking levels and timing of hatchery releases of juvenile salmon in estuaries are important in minimizing competition and predation (Myers 1980). Hatchery releases should avoid combining large concentrations of pink and chum salmon fry so as not to deplete food supplies. Conversely, releases during low predator abundance and good growing conditions—high food availability and warm temperature—could increase growth and

survival. Early releases of coho salmon could increase predation on pink and chum fry (Johnson 1974), especially fry <50 mm FL, if the releases coincide with fry migrations through the estuary.

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GROWTH THROUGH THE FIRST SIX MONTHS OF ATLANTIC COD, *GADUS MORHUA*, AND HADDOCK, *MELANOGRAMMUS AEGLEFINUS*, BASED ON DAILY OTOLITH INCREMENTS[1]

GEORGE R. BOLZ AND R. GREGORY LOUGH[2]

ABSTRACT

Daily growth increments of otoliths from larval and juvenile Atlantic cod and haddock were enumerated, and growth curves were derived describing the first six months of life. Growth for both species was best described by Gompertz-type curves. Inverse regressive methods were employed to construct general models with confidence limits for predicting age (days) for given standard lengths (mm) from hatching through the juvenile period. Microstructural analysis of the otoliths did not discern a settling check at the time when the fish would be expected to leave the pelagic lifestyle for the demersal one, which indicates that the transition is neither physiologically stressful nor abrupt.

Fluctuations in the year-class strength of fish stocks are thought to be determined by the rate of mortality during the first year of life (Moser 1981; Lough et al. 1985; Neilson and Geen 1986; and others). Calculation of reliable mortality rates, assessment of the influences of size-selectivity, and establishment of precise hatching dates and times during a given year when loss to recruitment is greatest are dependent upon accurate age and abundance estimates. Recently, investigators have suggested that mortality during the postlarval and juvenile periods may be as critical as that occurring in the egg and larval life stages (Cohen and Grosslein 1982; Sissenwine 1984). Investigation of this hypothesis by the Northeast Fisheries Center (NEFC) has been ongoing since 1984. Enumeration of daily growth increments deposited on fish otoliths provides the best method for the age determination of larvae and juveniles needed for generating growth curves and estimating mortality (Essig and Cole 1986). An excellent review of past and current methodologies employed in the study and application of otolith microstructure may be found in Campana and Neilson (1985).

Atlantic cod and haddock are both spring spawners on Georges Bank (Sherman et al. 1984) and have pelagic eggs and larvae that undergo similar development. Transformation to the juvenile life stage occurs around 20–30 mm SL, or 2–3 months from hatching (Fahay 1983). The transition from the pelagic to demersal habitat of the adults takes place sometime after transformation, usually by 6–8 cm in midsummer, and recent field observations by the NEFC indicates the transition is a gradual process with considerable variability.

In an earlier study by Bolz and Lough (1983), growth curves were developed for larval Atlantic cod and haddock based on otolith analysis that defined growth from hatching (4–5 mm SL) through the first two months of life (ca. 20 mm SL). Juvenile Georges Bank Atlantic cod and haddock are not fully vulnerable to bottom-trawl gear (Clark et al. 1982), and growth curves based on groundfish surveys conducted by the NEFC in the autumn and spring are inaccurate for fish younger than about six months of age. The primary goal of the work reported here was to derive age-at-length curves for field-caught Atlantic cod and haddock describing their growth from hatch until they are fully available to capture by bottom-trawl survey gear. A secondary objective was to determine if a check ring, a wide incremental band indicative of physiological or environmental changes, was deposited during the juvenile's transition from the pelagic to the demersal mode of life.

METHODS

Atlantic cod and haddock larvae and juveniles were collected on six cruises conducted by the NEFC's RV *Albatross IV* and RV *Delaware II* on

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Georges Bank during the springs of 1981, 1983, and 1984 and the summers of 1984 and 1985. Sample dates and station locations where larvae and juveniles were collected for otolith analysis are given in Table 1. The samples were collected with either 1) a continuous double-oblique haul using a 61 cm bongo net sampler (0.505 and 0.333 mm mesh) deployed to a maximum depth of 100 m (Posgay and Marak 1980), 2) a 1 m MOCNESS[3] fitted with nine 0.333 mm mesh nets which sampled discrete vertical strata from the bottom of the water column to the surface, 3) a 10 m MOCNESS (3 mm mesh) with five nets fished in the same manner as the 1 m MOCNESS (Wiebe et al. 1976, 1985), or 4) a Yankee 36 otter trawl towed for 30 minutes (Grosslein 1974). Stations with high densities of Atlantic cod and haddock larvae and juveniles in good condition were selected during the cruises for otolith analysis. The fish were removed immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae and juveniles representative of the entire size-range collected were selected for analysis. The standard length, as well as several other morphometric measurements of each larva or juvenile, was measured to the nearest 0.1 mm prior to removal of their otoliths. The 2 sagittae, 2 lapilli, and, when possible, 2 asterisci were dissected from the fish and, excepting juvenile sagittae, mounted whole on microscope slides with Permount[4]. The growth increments (Fig. 1A) on most of these otoliths were

[3]Multiple Opening/Closing Net and Environmental Sensing System.

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

TABLE 1.—Station information for Atlantic cod and haddock specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls (6B5), 1 m MOCNESS (0.333 mm mesh) discrete vertical hauls (1M3), 10 m MOCNESS (3.0 mm mesh) discrete vertical hauls (10M), and Yankee 36 otter trawl (Y36) during the 1981, 1983, and 1984 survey seasons.

Station	Lat. N	Long. W	Date	Time GMT (Night or day)	Gear	Bottom depth (m)	Number of fish	
							Cod	Haddock
1981	*Albatross IV* 81–03							
54	41°10′	67°06′	24 April	1235(D)	6B5	62	19	—
55	41°13′	67°02′	24 April	1330(D)	6B5	62	10	—
56	41°18′	66°58′	24 April	1450(D)	6B5	66	16	—
57	41°22′	66°55′	24 April	1630(D)	6B5	66	13	—
58	41°26′	66°51′	24 April	1840(D)	6B5	71	12	—
160	41°22′	67°00′	26 April	0645(N)	1M3	63	32	—
1981	*Albatross IV* 81–05							
190	40°57′	67°19′	22 May	0300(N)	1M3	76	—	8
197	40°55′	67°13′	25 May	1200(D)	1M3	80	—	16
205	40°55′	67°09′	26 May	1130(D)	1M3	80	—	6
211	41°11′	67°35′	27 May	1200(D)	1M3	49	—	27
215	41°12′	67°36′	27 May	2330(D)	1M3	40	—	19
1983	*Albatross IV* 83–03							
415	40°54′	67°32′	13 May	1816(D)	1M3	74	7	2
418	40°56′	67°35′	14 May	0456(D)	1M3	71	11	16
421	40°51′	67°34′	14 May	1026(D)	1M3	68	2	13
432	40°47′	67°26′	15 May	1636(D)	1M3	89	1	—
434	40°46′	67°24′	15 May	2229(D)	1M3	93	2	—
438	41°05′	67°47′	16 May	1147(N)	1M3	54	—	15
440	41°09′	67°54′	16 May	1646(N)	1M3	52	3	3
442	41°08′	67°48′	16 May	2222(N)	1M3	40	10	—
444	41°09′	67°55′	17 May	0504(N)	1M3	52	13	—
1984	*Albatross IV* 84–05							
519	41°19′	67°19′	18 June	0319(N)	10M	47	—	30
1984	*Delaware II* 84–07							
76	40°53′	66°22′	15 Aug.	1744(D)	Y36	66	1	1
85	41°50	66°26′	16 Aug.	1045(D)	Y36	78	—	1
88	41°49′	66°23′	16 Aug.	1430(D)	Y36	62	—	1
89	41°47°	66°18′	16 Aug.	1604(D)	Y36	68	—	4
90	41°47′	66°24′	16 Aug.	1715(D)	Y36	78	—	3
91	41°47′	66°30′	16 Aug.	1821(D)	Y36	72	—	1
93	41°45′	66°30′	16 Aug.	2024(D)	Y36	75	—	1
94	41°42′	66°25′	16 Aug.	2124(D)	Y36	75	—	1
98	41°47′	66°11′	17 Aug.	0249(N)	Y36	70	4	—
1984	*Albatross IV* 84–09							
18	41°49′	66°16′	12 Sept.	0845(N)	Y36	70	—	9
19	41°52′	66°21′	12 Sept.	0951(N)	Y36	90	1	12

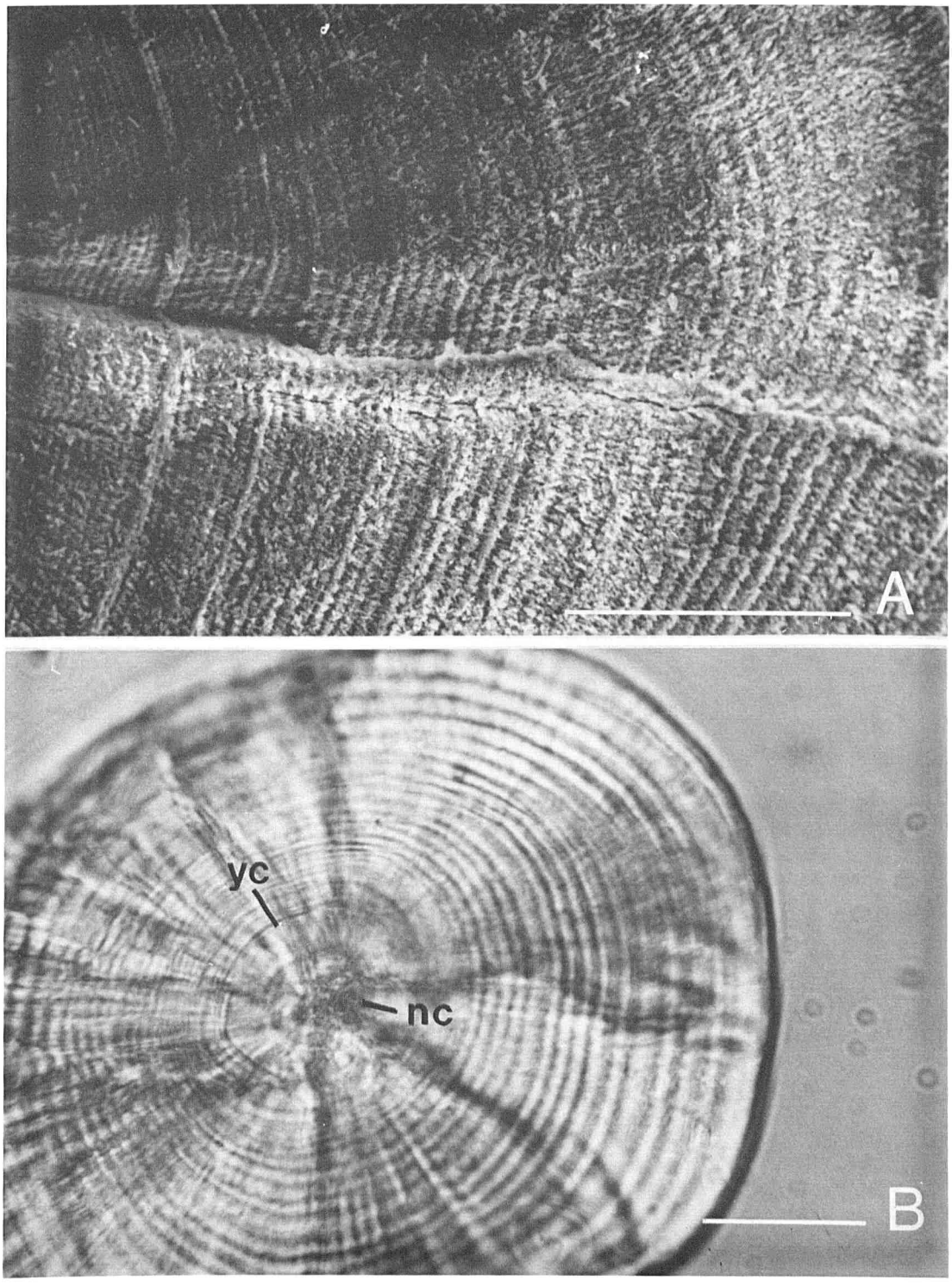


FIGURE 1.—A. Scanning electron micrograph for a portion of the sagitta from a 5-yr-old Atlantic cod, 79 cm SL, showing daily growth increments. Bar of photograph represents 100 μm. B. Sagitta from 47-d-old Atlantic cod larva, 13.3 mm SL (630×). Bar of photograph represents 20 μm. nc = nuclear check, yc = yolk-sac check.

discernible without any further preparation. Sagittae from fish >25 mm SL were mounted in epoxy resin and were ground, above and below, with carborundum paper (600 grit). The resulting thin section was secured to a microscope slide with epoxy resin and etched with 6% EDTA (pH 7.0). Both the grinding and etching procedures were monitored periodically by viewing the sagitta under a dissecting microscope.

The sagittae were then viewed under a Zeiss compound microscope with transmitted light. The number of growth increments were counted from the image projected by a drawing tube onto a Zeiss MOP Digital Image Analyzer System. Under transmitted light each growth increment was composed of a light and dark ring (Fig. 1B), which corresponded to the heavily calcified incremental zone and the organic-rich discontinuous zone of Watabe et al. (1982). Depending on the size of the otolith, magnifications used ranged from 400× to 1,000×. Three counts were made on one of the 2 sagittae from each larva or juvenile, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison, as were the 2 lapilli. The number of increments on the 2 asterisci also were enumerated. It was found in the previous study (Bolz and Lough 1983) that the asterisci were not detectable at hatching, in contrast to the sagittae and lapilli, but appeared later in the larval period. This was reflected in the asterisci having on average 27 fewer growth increments than the sagittae. In those instances where the sagittae and lapilli were particularly difficult to read, the number of asteriscal increments plus 27 was consulted as an additional check. Maximum and minimum diameters and planar surface area of the entire otolith were measured routinely on all sagittae, lapilli, and asterisci.

The differential shrinkage of Atlantic cod and haddock larvae and juveniles with respect to standard length was corrected using Theilacker's algorithm (1980), which is specified and discussed in Bolz and Lough (1983). All lengths referred to in the results and discussion portions of this paper are reported as corrected lengths.

RESULTS

Haddock Larval and Juvenile Growth

From analysis of the 189 larval and juvenile haddock, ranging from 3.5 to 123.4 mm SL, we found that growth was best described by a Gompertz-type curve. Previous uses of the Gompertz growth curve and methodology for fitting the curve are described in Pennington (1979), Lough et al. (1982), and Messieh et al. (1987). The variance was stabilized by using the natural log form of the growth equation, and parameters were derived by nonlinear estimation techniques resulting in the relationship:

$$\ln(L) = 1.1987 + 4.8438(1 - e^{-0.0088R}), \quad (1)$$

where L = standard length in mm, and
R = number of days (increments) from hatch.

A plot of the Gompertz curve fitted to the natural log of standard length vs. age in days is shown in Figure 2.

The predicted hatch-length from the curve of 3.32 mm falls within the range of previous studies (Colton and Marak 1969; Fahay 1983). An average growth rate of 0.24 mm/day (Table 2) for the first 30 days is also reasonable (Laurence 1978; Laurence et al. 1981) and agrees with the earlier study of Bolz and Lough (1983). As a generalized model the Gompertz equation described haddock growth through the first six months (175 days), at which point it intersected (Fig. 3) the von Bertalanffy growth curve generated from an analysis of adult haddock by Clark et al. (1982):

TABLE 2.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile haddock from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	3.32	3.22	3.41	0.14	4.22
10	4.99	4.88	5.11	0.20	4.01
20	7.27	7.13	7.41	0.26	3.58
30	10.25	10.07	10.42	0.34	3.32
40	14.03	13.80	14.26	0.42	2.99
50	18.70	18.39	19.02	0.51	2.78
60	24.34	23.89	24.80	0.61	2.55
70	30.98	30.34	31.63	0.71	2.32
80	38.63	37.74	39.53	0.82	2.12
90	47.27	46.08	48.51	0.91	1.95
100	56.88	55.30	58.50	1.01	1.77
110	67.37	65.35	69.45	1.09	1.63
120	78.67	76.14	81.28	1.17	1.49
130	90.66	87.56	93.86	1.23	1.35
140	103.23	99.52	107.08	1.28	1.23
150	116.26	111.88	120.81	1.32	1.14
160	129.63	124.54	134.92	1.35	1.04
170	143.21	137.38	149.28	1.36	0.95
180	156.88	150.29	163.76	1.37	0.87
190	170.54	163.17	178.25	1.36	0.80
200	184.09	175.92	192.63	1.35	0.73

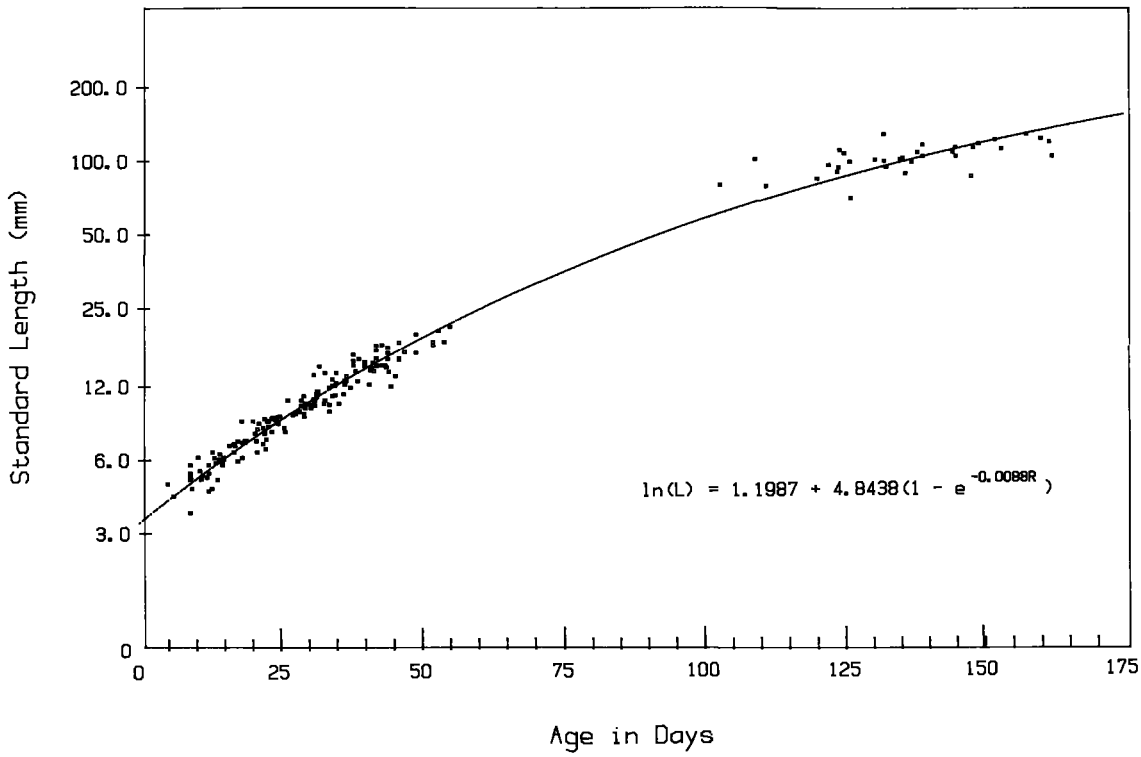


FIGURE 2.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 189 larval and juvenile haddock collected on Georges Bank.

$$L = 738.0(1 - e^{-0.3763[(R+D)/365-0.1649]}), \quad (2)$$

where D = Julian date of hatch.

Based on the 1981 season, an average hatch-date of 15 April (D = 105) was employed in the present model. An average length of 19.9 cm would have been attained on 1 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

Atlantic Cod Larval and Juvenile Growth

Although there were few larger individuals amongst the 157 larval and juvenile Atlantic cod examined, the apparent pattern was similar to that seen in haddock. A Gompertz growth curve also provided a good fit when the natural log of standard length (range: 4.6–104 mm) was plotted (Fig. 4) against age in days (range: 7–151):

$$\ln(L) = 1.3915 + 6.2707(1 - e^{-0.0053R}). \quad (3)$$

The predicted hatch-length of 4.02 mm was within known limits (Colton and Marak 1969). The average growth rate of 0.21 mm/day (Table 3) through the first month was slightly lower than that of haddock, which is consistent with previous findings (Bolz and Lough 1983). At approximately 192 days the larval and juvenile growth curve intersected the von Bertalanffy curve calculated for adult Atlantic cod by Penttila and Gifford (1976):

$$L = 1481.0(1 - e^{-0.1200((R+D)/365-0.6160)}). \quad (4)$$

For purposes of the model a mean hatch-date of 15 March (D = 74) was assumed. An average Atlantic cod would be expected to have achieved a length of 26.1 cm by 1 January (Fig. 5).

Predictability

Since it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to predict age from a given length,

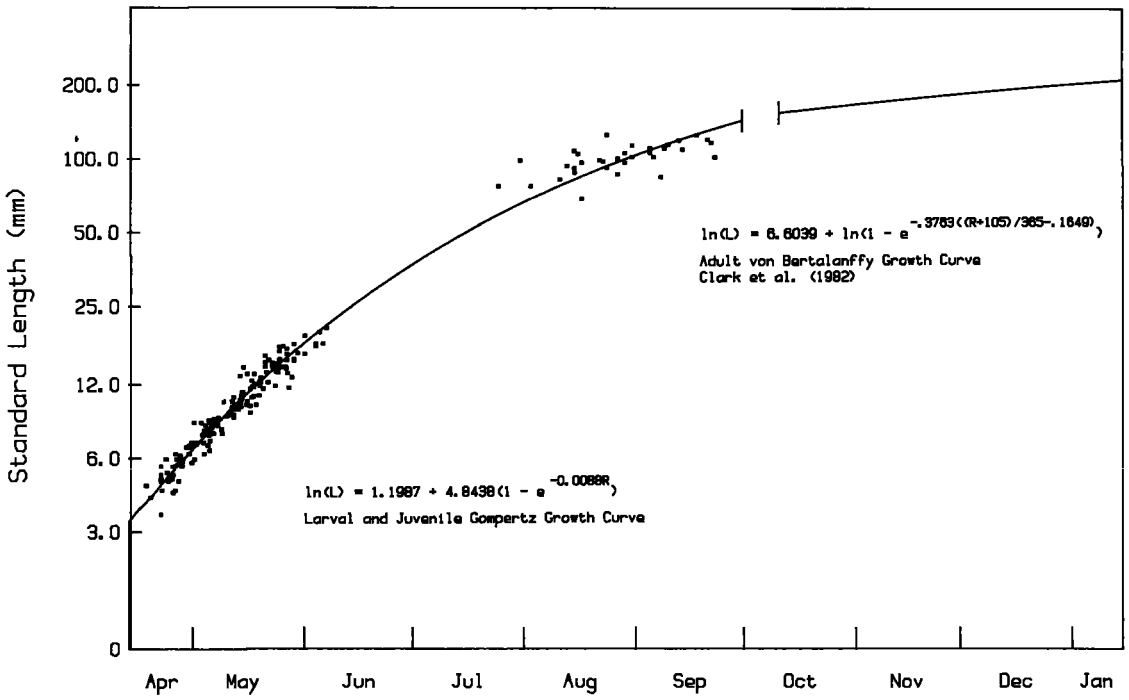


FIGURE 3.—Haddock growth model with an assumed mean hatch-date of 15 April projected through mid-January. An average length of 19.9 cm would have been attained on 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.

inverse regression (Draper and Smith 1966) was performed on the Atlantic cod and haddock growth curves to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for haddock was

$$\frac{X_u}{X_l}] = \frac{\ln(1 - (X_0 \pm 0.023t(((X_0 - 0.2990)^2/7.7959) + (1 + 1/n))^{1/2}))}{-0.0088} \quad (5)$$

where X_u and X_l = upper and lower confidence limits,
$X_0 = 1 - e^{-0.0088R}$, and
n = sample size.

Figure 6 shows the fitted growth curve bracketed by 95% confidence intervals.

Performing the same calculations on the Atlantic cod growth curve yielded the relationship:

$$\frac{X_u}{X_l}] = \frac{\ln(1 - (X_0 \pm 0.022t(((X_0 - 0.1918)^2/0.9294) + (1 + 1/n))^{1/2}))}{-0.0053} \quad (6)$$

where $X_0 = 1 - e^{-0.0053R}$.

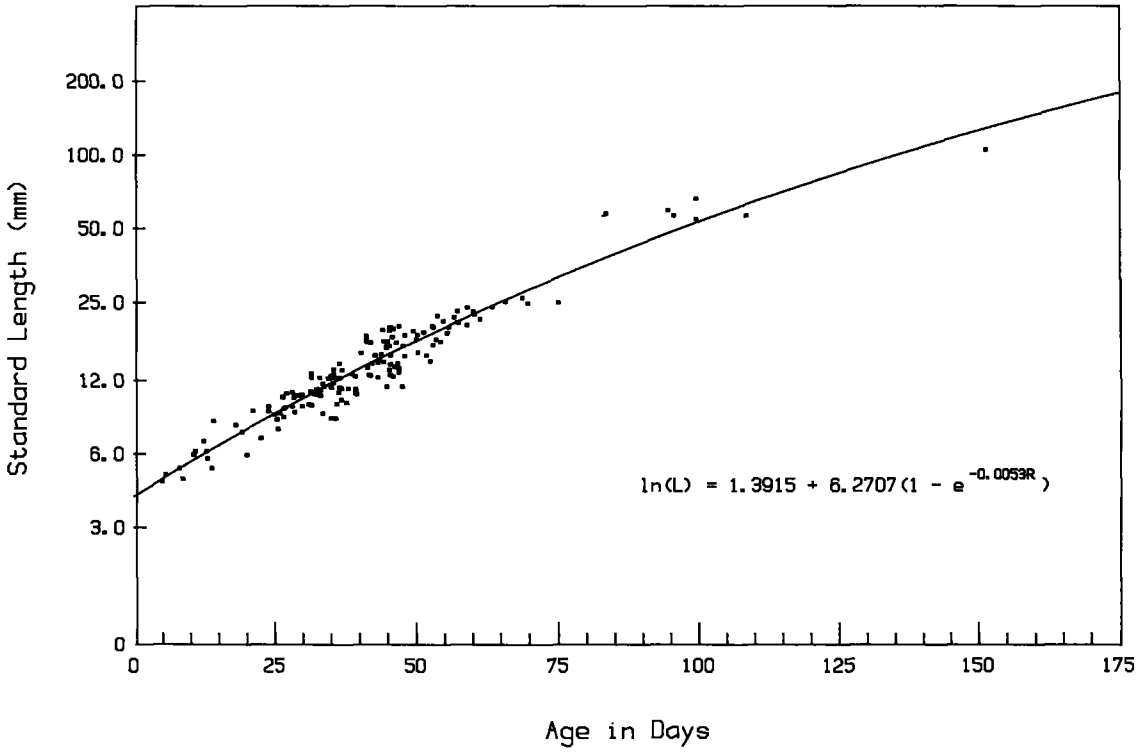


FIGURE 4.—Gompertz growth curve and equation fitted to plot of ln standard length and number of otolith increments (estimated age in days) for 157 larval and juvenile Atlantic cod collected on Georges Bank.

TABLE 3.—Mean standard length at age, 95% confidence limits, and growth rate (mm/day and %/day) of larval and juvenile Atlantic cod from hatch through 200 days estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/day)	Growth rate (%/day)
		Lower	Upper		
0	4.02	3.79	4.27	0.13	3.37
10	5.56	5.31	5.82	0.18	3.24
20	7.55	7.30	7.82	0.23	3.05
30	10.11	9.85	10.37	0.29	2.87
40	13.32	13.03	13.62	0.36	2.70
50	17.31	16.88	17.75	0.44	2.60
60	22.19	21.48	22.92	0.54	2.43
70	28.08	26.95	29.26	0.64	2.31
80	35.11	33.40	36.91	0.76	2.19
90	43.39	40.91	46.03	0.90	2.10
100	53.05	49.58	56.77	1.04	1.98
110	64.18	59.48	69.26	1.19	1.87
120	76.90	70.69	83.65	1.35	1.77
130	91.27	83.26	100.05	1.52	1.68
140	107.38	97.24	118.57	1.70	1.58
150	125.27	112.65	139.30	1.88	1.51
160	144.99	129.52	162.30	2.06	1.43
170	166.55	147.85	187.61	2.25	1.35
180	189.95	167.61	215.26	2.43	1.28
190	215.17	188.79	245.24	2.61	1.22
200	242.18	211.34	277.52	2.79	1.16

Figure 7 shows the Atlantic cod growth curve bracketed by 95% confidence intervals. Tables 4 and 5 provide predicted ages of Atlantic cod and haddock for given standard lengths with 70% and 95% confidence limits.

Otolith Growth

In the earlier study of larval Atlantic cod and haddock (Bolz and Lough 1983), it was found that the sagittal rings (one incremental and one discontinuous zone) were segregated into distinct regions separated by thicker, darker discontinuous zones referred to as checks or check rings. Two "heavy rings" were noted in the larvae: 1) a nuclear check surrounding a central, amorphous core and 1 or 2 irregular rings, and 2) a yolk-sac check 2–8 increments farther outward (Fig. 1B). The present study corroborated the existence of these two checks. Although each otolith was carefully examined for the presence of a settling check, no regularly occurring heavy ring could be discerned beyond the yolk-sac check in either the haddock or the Atlantic cod juveniles. It should,

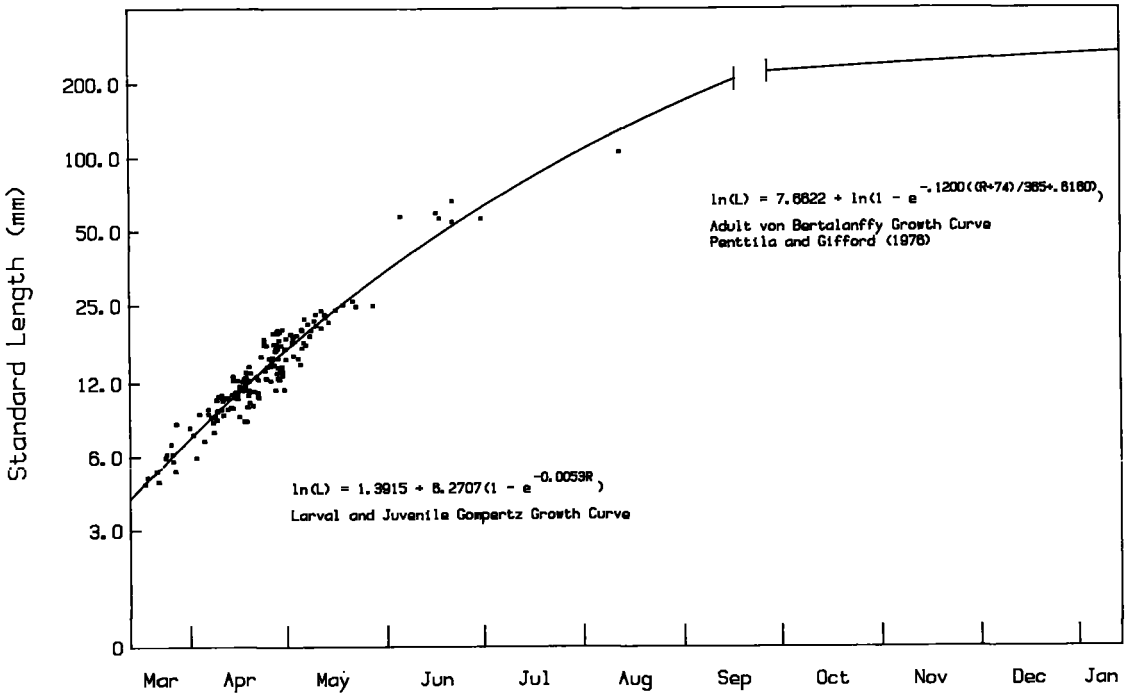
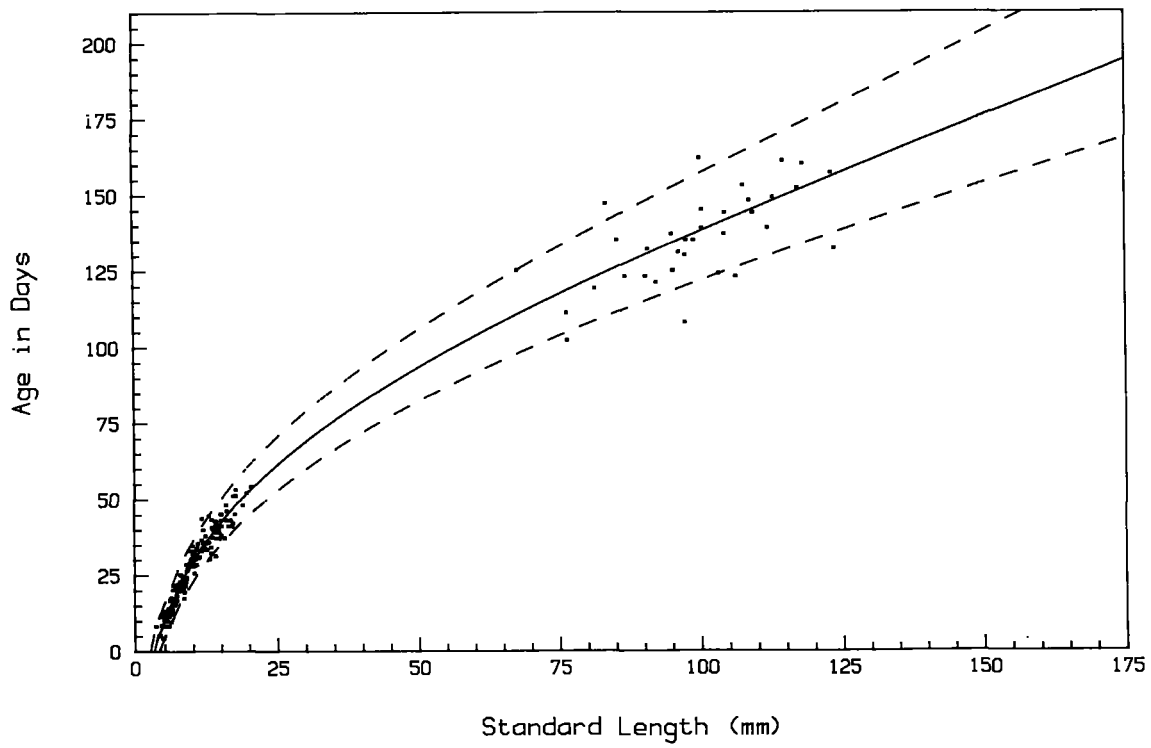


FIGURE 5.—Atlantic cod growth model with assumed mean hatch-date of 15 March projected through mid-January. An average length of 26.1 cm would have been attained by 01 January, by fisheries science convention the date at which an individual is considered to be 1-year-old.



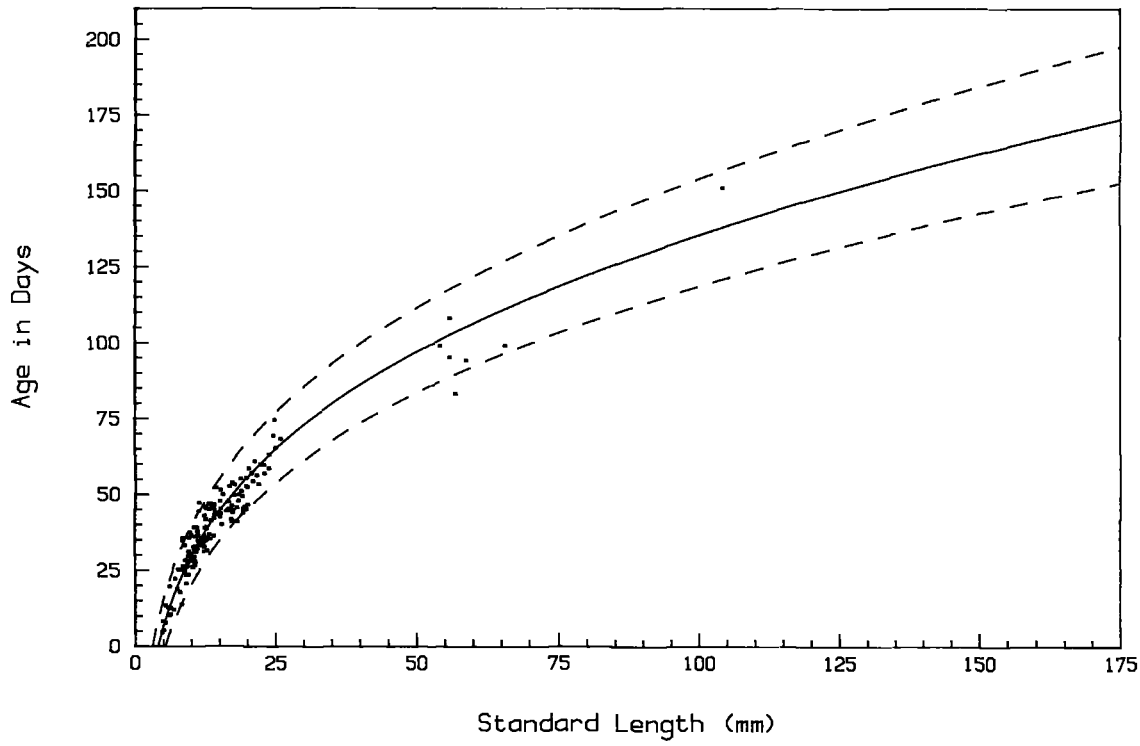


FIGURE 7.—Inverse regression of Atlantic cod growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

however, be noted that the size range available for study limited the search for a settling check to individuals >90 mm SL and does not preclude the possibility that thinner, less discernible checks may be found when greater numbers of juveniles 50–90 mm SL are analyzed.

In both haddock and Atlantic cod diametral growth (μm) of the sagittae, lapilli, and asterisci was linearly related to standard length (mm) throughout the larval and juvenile periods. The high correlation ($r > 0.98$) of this relationship and its good agreement with measurements made by Bergstad (1984) would allow the sagittal diameter to be used as a check on the predictability model outlined in Equations (5) and (6) for estimating age from standard length. Estimated ages for haddock larvae and juveniles based on maximum otolith diameters may be obtained with the following equation:

$$Y = 28.390 + 2.413X_1 + 21.561X_2 + 73.841X_3 \quad (7)$$

where Y = estimated age in days,
X_1 = sagittal diameter in mm,
X_2 = lapillus diameter in mm, and
X_3 = astericus diameter in mm.

Table 6 provides a comparison of estimated ages derived from otolith diameters with observed ages derived from the number of daily increments. Although multiple regression analysis using the three otolith diameters yielded a high correlation coefficient ($r = 0.9890$) and nonsignificant t-values, the 95% confidence limits are quite broad (±2 weeks) and should be used with caution. Use of the sagittal diameter alone ($Y = 35.945 + 18.484X_1$) provided a good fit ($r = 0.9861$) for juveniles >90 mm SL but was a poor age predictor for younger fish. If only the sagitta is available for analysis, the relationship:

FIGURE 6.—Inverse regression of haddock growth curve with 95% confidence intervals for predicting age in days for a given standard length (mm).

TABLE 4.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile haddock for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	10.0	7.1	13.0	4.4	15.9
10	29.3	25.8	32.8	22.7	36.2
15	42.3	38.4	46.3	34.9	50.1
20	52.5	48.2	56.9	44.4	61.1
25	61.1	56.5	65.8	52.4	70.4
30	68.6	63.8	73.7	59.4	78.7
35	75.4	70.3	80.8	65.7	86.1
40	81.7	76.2	87.4	71.4	93.0
45	87.5	81.7	93.5	76.7	99.5
50	92.9	86.9	99.3	81.6	105.6
55	98.1	91.8	104.8	86.3	111.4
60	103.1	96.5	110.0	90.7	117.0
65	107.8	101.0	115.1	95.0	122.4
70	112.4	105.3	120.0	99.0	127.6
75	116.8	109.4	124.8	103.0	132.7
80	121.1	113.5	129.4	106.8	137.7
85	125.3	117.4	133.9	110.4	142.6
90	129.5	121.2	138.4	114.0	147.4
95	133.5	124.9	142.8	117.5	152.2
100	137.5	128.6	147.1	121.0	156.9
105	141.4	132.2	151.4	124.3	161.6
110	145.2	135.8	155.6	127.6	166.2
115	149.0	139.3	159.8	130.9	170.8
120	152.8	142.7	163.9	134.1	175.4
125	156.6	146.1	168.1	137.2	180.0
130	160.3	149.5	172.2	140.4	184.6
135	164.0	152.9	176.3	143.4	189.2
140	167.6	156.2	180.4	146.5	193.9
145	171.3	159.5	184.6	149.5	198.5
150	175.0	162.8	188.7	152.5	203.2
155	178.6	166.0	192.8	155.5	207.9
160	182.3	169.3	197.0	158.5	212.7
165	185.9	172.6	201.2	161.4	217.5
170	189.6	175.8	205.4	164.3	222.4
175	193.3	179.0	209.6	167.3	227.4

TABLE 5.—Predicted age in days with 70% and 95% confidence limits of larval and juvenile Atlantic cod for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% confidence limits		95% confidence limits	
		Lower	Upper	Lower	Upper
5	6.7	2.1	11.3	−2.1	15.7
10	29.6	24.5	34.8	19.9	39.8
15	44.5	39.0	50.1	34.0	55.5
20	55.8	49.9	61.8	44.7	67.6
25	65.0	58.9	71.3	53.4	77.5
30	72.9	66.5	79.6	60.8	86.0
35	79.9	73.2	86.8	67.3	93.5
40	86.1	79.2	93.3	73.1	100.3
45	91.8	84.7	99.2	78.3	106.5
50	97.0	89.7	104.7	83.2	112.2
55	101.9	94.3	109.8	87.6	117.6
60	106.4	98.7	114.6	91.8	122.6
65	110.7	102.7	119.1	95.7	127.3
70	114.7	106.6	123.3	99.4	131.8
75	118.6	110.3	127.4	102.9	136.1
80	122.3	113.8	131.3	106.3	140.2
85	125.8	117.1	135.0	109.5	144.1
90	129.2	120.3	138.6	112.5	147.9
95	132.4	123.4	142.0	115.5	151.6
100	135.6	126.4	145.4	118.3	155.1
105	138.6	129.2	148.6	121.0	158.6
110	141.5	132.0	151.7	123.7	161.9
115	144.4	134.7	154.8	126.3	165.1
120	147.2	137.3	157.7	128.7	168.3
125	149.9	139.9	160.6	131.1	171.3
130	152.5	142.3	163.4	133.5	174.3
135	155.1	144.8	166.1	135.8	177.3
140	157.6	147.1	168.8	138.0	180.2
145	160.0	149.4	171.4	140.2	183.0
150	162.4	151.6	174.0	142.3	185.7
155	164.8	153.8	176.5	144.4	188.5
160	167.1	156.0	179.0	146.4	191.1
165	169.3	158.1	181.4	148.4	193.7
170	171.5	160.2	183.8	150.4	196.3
175	173.7	162.2	186.2	152.3	198.8

$$Y = 11.875 + 112.654X_1,\ r = 0.9129 \quad (8)$$

should be used for the larval and postlarval period.

The equation for the estimated ages of larval and juvenile Atlantic cod (Table 7) is as follows:

$$Y = 48.202 + 8.628X_1 - 121.908X_2 + 139.733X_3,$$

$$r = 0.9292. \quad (9)$$

When using only the sagittal diameter, the following relationship should be applied to larvae and postlarvae:

$$Y = 19.364 + 89.560X_1,\ r = 0.8659. \quad (10)$$

Unlike the tedious laboratory methods needed for the enumeration of otolith increments, gross measurements on a limited number of juvenile otoliths could be performed at sea.

DISCUSSION

Despite the tedious methodology required for enumerating daily growth increments in larval and juvenile otoliths, the present work suggests that it is feasible to construct age-length keys for Atlantic cod and haddock similar to those commonly applied in adult population studies (Clark et al. 1982). The value of such growth data is based on several assumptions, however. Since all conclusions drawn depend upon it, reasonable assurance of the day-increment relationship in the species being investigated is critical (Beamish and McFarlane 1987; Geffen 1987). Confidence in the growth models generated here for Atlantic cod and haddock may be found in the following inferences: 1) the predicted hatch lengths of 3.32 mm for haddock and 4.02 mm for Atlantic cod fall within known limits; 2) a high correlation for the length-at-age data with the rearing experiments of Laurence et al. (1981); and 3) the smooth-

TABLE 6.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile haddock compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	1.5	−12.3	15.4
10.0	11.3	−2.5	25.1
20.0	21.1	7.4	34.9
30.0	30.9	17.2	44.6
40.0	40.7	27.0	54.4
50.0	50.5	36.8	64.2
60.0	60.3	46.7	73.9
70.0	70.1	56.5	83.7
80.0	79.9	66.2	93.6
90.0	89.7	76.0	103.3
100.0	99.5	85.8	113.1
110.0	109.3	95.6	122.9
120.0	119.0	105.3	132.8
130.0	128.8	115.1	142.6
140.0	138.6	124.8	152.5
150.0	148.4	134.5	162.3
160.0	158.2	144.3	172.2
170.0	168.0	154.0	182.0
180.0	177.8	163.7	191.9

TABLE 7.—Estimated age in days based on otolith diameters with 95% confidence limits for larval and juvenile Atlantic cod compared with observed age derived from number of daily increments.

Observed age (d)	Estimated age (d)	95% confidence limits	
		Lower	Upper
0.0	7.1	−6.9	21.1
10.0	15.8	2.1	29.5
20.0	24.5	11.0	38.0
30.0	33.2	19.9	46.5
40.0	41.9	28.7	55.1
50.0	50.6	37.5	63.8
60.0	59.3	46.2	72.5
70.0	68.0	54.8	81.2
80.0	76.7	63.4	90.1
90.0	85.4	71.9	98.9
100.0	94.1	80.4	107.9
110.0	102.8	88.8	116.9
120.0	111.6	97.2	125.9
130.0	120.3	105.5	135.0
140.0	129.0	113.8	144.1
150.0	137.7	122.1	153.3
160.0	146.4	130.3	162.5
170.0	155.1	138.5	171.7
180.0	163.8	146.6	180.9

ness with which the larval and juvenile curves flow into those independently developed for the adults (Clark et al. 1982; Penttila and Gifford 1976).

The predictive models for Atlantic cod and haddock have to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4, 5) must be kept in mind. Natural variability of length-at-age and difficulty in the preparation and reading of otoliths increases as the fish becomes older and makes precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual haddock at the 70% confidence level decreases from ±3 days at 5 mm SL to ±2 weeks at 175 mm. In spite of this problem, otolith aging of field-caught larvae and juveniles provides a degree of precision not possible with indirect methods based on size-frequency analyses (Ebert 1973). Refinement of the estimated means and the reduction and stabilization of the variance should result as a greater number of otoliths are analyzed in the future.

Microstructural examination of larval Atlantic cod and haddock otoliths clearly delineated check rings related to hatching and yolk-sac absorption (Bolz and Lough 1983). Both of these transitions are abrupt, and the dark, thick discontinuous zones readily observable on the otoliths are a reflection of metabolic disturbances undergone at these times. Although additional check rings were noted in 3 or 4 of the juvenile otoliths, there was no regularity with respect to age of their occurrence. In these individuals the checks were probably the result of physiological trauma induced by disease or injury since calcium carbonate secretion ceases not only with the metabolic changes accompanying transitional phases but during times of stress (Morales-Nin 1987). It was suspected that a distinct check, similar to the settling check found by Victor (1982) in the bluehead wrasse, *Thalassoma bifasciatum*, would be found demarcating the transition from the pelagic to the demersal mode of life with its accompanying changes in diet and activity levels. No check rings were found in the transition period (50–100 days) on the otoliths analyzed. This suggests that an abrupt metabolic disturbance does not occur at this phase of the fish's life and that settling near the bottom takes place over an extended period of time (1–2 months) even for individual fish. This agrees with a preliminary finding for Scotian Shelf gadoids by Campana and Neilson (1985). However, in a recent study by Mahon and Neilson (1987) on the gut contents of Scotian Shelf haddock, they concluded that the transition from pelagic to demersal life occurred relatively suddenly, less that a month for the individual fish. Apparently, change to the demersal life stage is not stressful for Atlantic cod and haddock, at least as a metabolic manifestation recorded in their otoliths.

When used in conjunction with length-frequency data collected throughout the year, the Atlantic cod and haddock growth curves presented in this report should allow accurate estimates of the following: 1) peak hatching dates, 2) the number of cohorts produced within a given season, 3) intraseasonal changes in growth and mortality rates of cohorts, and 4) which part of the spawning curve the recruits originated from (Methot 1983). In the future year-to-year comparison of deviations in these estimates could lead to the construction of viable recruitment models permitting the early prediction of year-class strength.

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THE RELATION BETWEEN SPAWNING SEASON AND THE RECRUITMENT OF YOUNG-OF-THE-YEAR BLUEFISH, *POMATOMUS SALTATRIX*, TO NEW YORK[1]

ROBERT M. NYMAN[2] AND DAVID O. CONOVER[3]

ABSTRACT

The association between oceanic spawning season and the recruitment of young-of-the-year (YOY) bluefish, *Pomatomus saltatrix*, to the inshore waters of New York was studied by estimating the spawn dates of recruited fish collected in the shore zone from the number of growth increments in their otoliths. Field collections on the south shore of Long Island showed that recruitment of 3–6 cm fork length fish occurred as a distinct pulse during the last week of May in 1985 and the second week of June in 1986. Length-frequency distributions were generally unimodal and most fish collected later could be attributed to this one recruitment episode. The frequency of otolith ring deposition in YOY bluefish was determined by marking the otoliths of field-caged fish with an injection of tetracycline, and then periodically subsampling these over the ensuing 61-day period. Regression analysis indicated a 1:1 relation between the number of days since marking and the number of rings beyond the mark. Back-calculation to the time of first ring deposition revealed that field-collected YOY bluefish from Long Island were spawned primarily in the March–April spawning season reported to occur south of Cape Hatteras. Relatively few fish were collected from the summer spawning season that reportedly occurs in the Middle Atlantic Bight. Almost all of these summer-spawned fish were collected from the Hudson River.

The bluefish, *Pomatomus saltatrix*, supports a major recreational fishery along the Atlantic coast of the United States. In 1985, more bluefish by weight were caught than any other marine fish, accounting for over 24% of the total marine recreational catch (U.S. Department of Commerce 1986). Despite the importance of bluefish to the recreational fishery, very little is known of its early life history.

Bluefish are found over different portions of the continental shelf from Florida to Nova Scotia at various times of the year (Bigelow and Schroeder 1953; Wilk 1977; Gilmore 1985). Based on descriptions of the temporal and spatial abundance of larvae, Kendall and Walford (1979) suggested that there are primarily two distinct spawning periods and regions: a spring spawning in the South Atlantic Bight at the edge of the Florida Current (see also Collins and Stender 1987), and a summer spawning in the Middle Atlantic Bight midway over the continental shelf (see also Morse et al. 1987). They further proposed that the spring-spawned larvae are transported northward in the slope waters and then move inshore, spending their first summer in the bays and estuaries of the Middle Atlantic Bight. Summer-spawned larvae, according to Kendall and Walford, spend their first summer at sea or enter the estuaries of the Middle Atlantic Bight only briefly before migrating southward with the onset of winter. A minor spawning season extending from September to November off the coast of Georgia and Florida (Collins and Stender 1987) involves fish resident to the South Atlantic Bight (Kendall and Walford 1979).

The purpose of this study is to evaluate Kendall and Walford's hypothesis by back-calculating the spawn dates of young-of-the-year (YOY) bluefish that have recruited to inshore waters, from the number of growth increments in their otoliths. First, we describe the timing and pattern of recruitment of YOY bluefish to one segment of the mid-Atlantic coastline: Long Island, NY. If spawning is episodic, and if YOY bluefish from each spawning period enter New York waters, then length-frequency distributions of field collections should be multimodal. Next, we verify that otolith increment deposition has a daily peri-

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odicity in *P. saltatrix*. Finally, the spawning season(s) of YOY bluefish recruiting to New York is determined by ageing and back-calculating to the date of first ring deposition.

METHODS

Seine Collections

The temporal abundance and length-frequency distribution of YOY bluefish was estimated by seining 2–4 times per month from April to October at several sites on Long Island and in the Hudson River (Fig. 1). In 1985 and 1986, three sites in Great South Bay on the south shore of Long Island were sampled: Smith Point County Park, Fireplace Neck, and the Carmans River. Seining was conducted with a 0.6 cm mesh, 30 m net set from shore, either on foot or from a small boat. Water temperature was recorded at each site and date. In 1986, a site on the north shore of Long Island, Setauket Harbor, was also sampled. A few samples were taken in the fall by angling with rod and reel. All specimens were frozen for later measurement of fork length (FL) and weight, and extraction of otoliths.

Additional specimens captured in 1986 from Jamaica Bay and the Hudson River were provided by the New York Department of Environmental Conservation (NYDEC). Their sampling was conducted with a 60 m seine (1.2 cm mesh) set from a boat.

Otolith Preparation and Analysis

The sagittae were mounted concave side down on a glass microscope slide with cyanoacrylate (instant glue). Two layers of masking tape were applied on either side of the otolith. The slide was then turned upside-down and sanded on a strip of wet 1200 grit wet-dry sandpaper. The masking tape ensured that the otolith was sectioned on a consistent plane and helped prevent grinding past the nucleus. Once the nucleus was reached, the otolith was polished on wet felt, using levigated alumina polishing compound. Three replicate counts of each otolith were made under a Zeiss[4] compound microscope with transmitted polarized light at 125–312×. If the three counts differed by more than 10% (which occurred in about 1 out of every 10 otoliths), an additional count was made and the outlier discarded. The three final counts were then averaged. The total length of each otolith was measured (nearest 0.1 mm) with a dissecting microscope using an ocular micrometer.

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

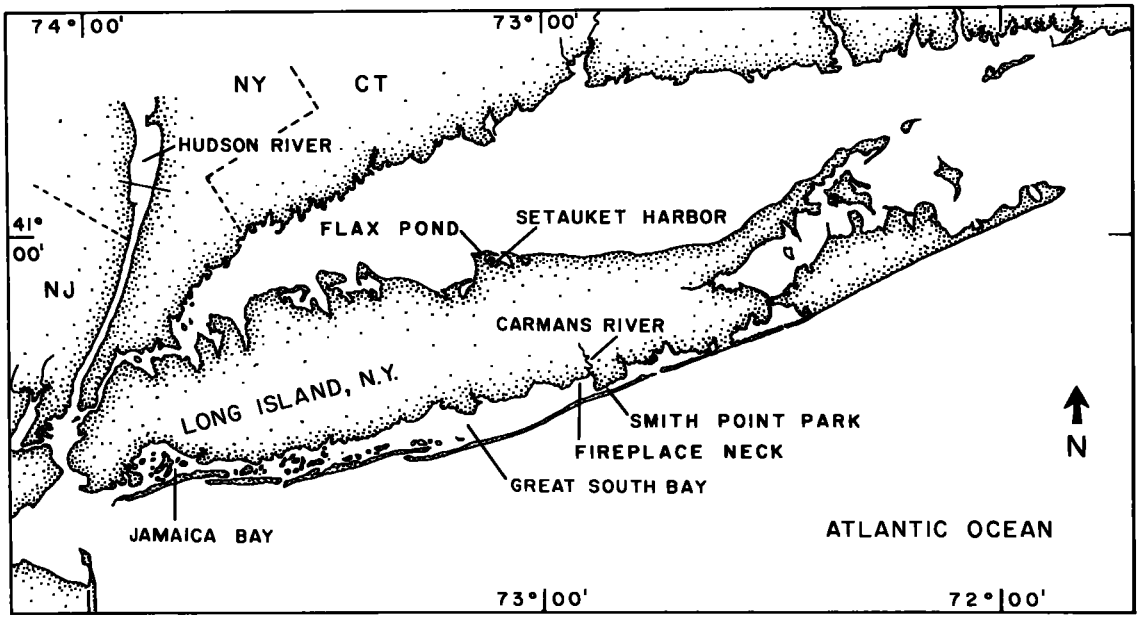


FIGURE 1.—Map of the study area with sampling locations as indicated.

Frequency of Ring Deposition

The frequency of growth ring deposition was determined by marking the otoliths of fish with tetracycline and then subsampling the marked fish at various periods of time thereafter (Campana and Neilson 1982). Sixty YOY bluefish (7–10 cm FL) were captured by seine in Flax Pond, Old Field, NY (Fig. 1) and were transported to the Flax Pond Laboratory of SUNY Stony Brook. The fish were anesthetized in a solution of MS-222 (30 mg/L) and given an intraperitoneal injection of tetracycline (100 mg/kg of fish). After injection, all fish were placed in a 1.3 × 1.3 m cylindrical floating cage constructed out of 5 mm plastic mesh and anchored in Flax Pond. The fish were fed chopped *Menidia menidia* twice a day, and dead bluefish were removed daily. Samples of 5–10 healthy fish were periodically taken from the cage using a dip net and frozen until the otoliths could be excised. The experiment was terminated 61 days after the injections.

After preparation as described above, the tetracycline-treated otoliths were viewed on a Zeiss compound microscope using reflected ultraviolet (UV) light at 160–400×. Tetracycline fluoresces upon exposure to UV light, thus enabling the location of the marked ring to be determined. The UV light was then turned off, and the number of rings from the mark to the edge of the otolith was counted under transmitted white light. Each otolith preparation was coded so that the reader did not know the true age. Three replicate counts were conducted on each otolith.

RESULTS

Temporal Abundance and Length Frequency

Great South Bay

The appearance of YOY bluefish in the shore zone was abrupt in both years of the study. In 1985, no YOY bluefish were caught in weekly samples until 28 May when a catch per unit effort (CPUE = no. fish per seine haul) of 14.0 was recorded (Fig. 2a). Corresponding water temperature was about 20°C. CPUE declined steadily thereafter through October with two exceptions: the large collections on 10 and 28 July were each due to an unusually large number of fish in single seine hauls in the Carmans River. In 1986, YOY bluefish were first caught on 10 June when the water temperature was 24°C. The maximum CPUE (45.3) was obtained on 16 June and was followed by a decrease in CPUE in subsequent collections (Fig. 2b).

Length-frequency distributions in 1985 showed the progression of a single mode through mid-August (Fig. 3a). Newly recruited fish in late May were 3–6 cm FL. Subsequent samples showed an increase in the mean and range of fish lengths, probably due to somatic growth of the initial recruits. There was no evidence of new 3–6 cm recruits entering the shore zone later in the year (Fig. 3a). Although seining continued until November, very few YOY bluefish were caught after August. An additional sample (n = 8) taken on 16 September by angling from a pier on Great South Bay had a mean fork length of 17.8 cm and a range of 14.6–19.5 cm. Length-frequency data from 1986 (Fig. 3b) show a very similar pattern to that in 1985: a single length mode appears in June and these fish increase in size through the summer. Few YOY bluefish were caught in August, September, or October.

Size at recruitment to the shore zone was similar in both years of our study: mean length of the 1985 and 1986 year classes at first appearance in the shore zone was 4.6 and 4.5 cm respectively (Fig. 4). However, because the 1986 year class first appeared in the shore zone two weeks later than did the 1985 year class (Fig. 2), the mean lengths of 1986 year class were less than those of 1985 on comparable dates in June and early July. By mid-July, however, this difference in mean length of the two year classes was no longer apparent. Both year classes reached a size of about 13–14 cm by late August when they rarely appeared in our seine collections.

Setauket Harbor

In 1986, the YOY bluefish did not appear on the north shore of Long Island at Setauket Harbor until 3–6 weeks after they first appeared in Great South Bay. Collections at Setauket Harbor were small at first with only one individual being caught on 1 July and three on 8 July. It was not until 22 July that catches similar in number to those in Great South Bay were being obtained. These fish had similar mean lengths (10.2 cm, n = 87, on 22 July; 11.9 cm, n = 22, on 5 August; 13.9 cm, n = 17, on 20 August) to those on comparable dates from Great South Bay (cf. Fig. 4). Length-frequency distributions by date were unimodal.

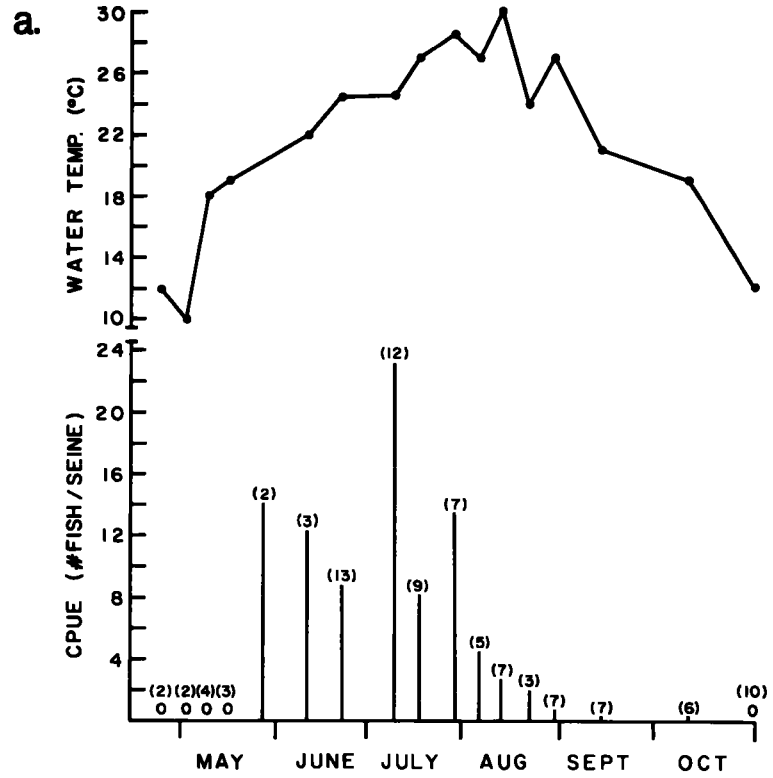


FIGURE 2.—Catch per unit effort (CPUE) of YOY bluefish from Great South Bay, NY, plotted with the mean water temperature

Jamaica Bay and the Hudson River

The length-frequency distributions of YOY bluefish from Jamaica Bay in June, July, and August were similar to those from Great South Bay (Fig. 5). Fish lengths in June were unimodal. Subsequent collections contained progressively larger fish that were also unimodal in length distribution.

Sampling in the Hudson River began on 16 July 1986 and continued through 8 October. The size ranges of YOY bluefish in the July and August samples were similar to those from Great South Bay, although the length distribution on 30 July appears bimodal (Fig. 6). The length distributions from the 10 and 23 September collections were especially broad. In particular, the 23 September sample contained a group of fish that were much smaller (10–14 cm FL) than the mean size at this time in Great South Bay (Fig. 4), together with a second group of larger fish that correspond more closely in size with those collected elsewhere (18–24 cm).

Frequency of Ring Deposition

In tetracycline-injected YOY bluefish, the number of rings beyond the tetracycline mark (Y) and the number of days after injection (X) had a 1:1 correspondence (Fig. 7). The relationship was described by the equation $Y = 0.971X - 0.287$ ($n = 27, r = 0.996$). The slope did not differ significantly from 1.0 (t-test, $P > 0.1$).

Growth rate of the caged fish was slightly greater than that of field fish and survival was high (80%) with mortalities occurring only in the first few days of the 61-d experiment. The increase in mean fork length was 1.7 mm/day among the caged fish, as compared with about 1.3 mm/day for fish from field collections during the same time period (Fig. 4). Hence, the caged fish did not appear to be adversely affected by confinement.

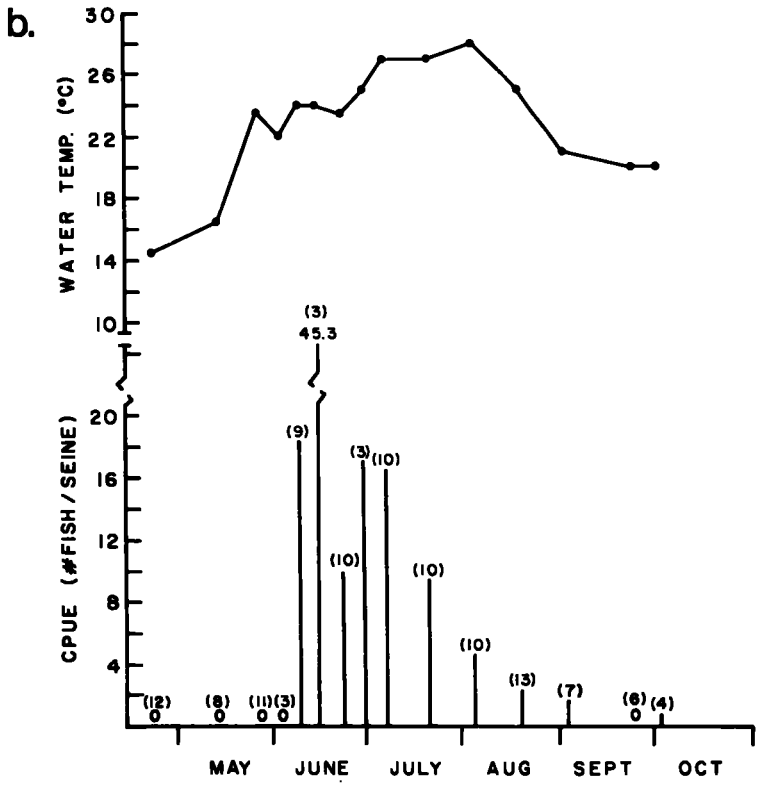


FIGURE 2.—*Continued*—on each sampling date. (a) 1985; (b) 1986. Number of seine hauls is in ().

Back-Calculated Date of First Ring Deposition

A representative sample of 169 YOY bluefish (n = 88 from 1985, n = 81 from 1986) captured in Great South Bay were aged by counting the total number of otolith rings. The date of first ring deposition for each aged fish was then calculated based on the date of capture. In both 1985 and 1986, the dates of first ring deposition for YOY bluefish were predominantly in March and April (Fig. 8a, b).

Four fish from each of the two apparent length modes in the 30 July collection from the Hudson River (Fig. 6) were aged to determine if these represented a difference in spawning season. The fish examined were 7.8–13.8 cm in size, and back-calculated dates of first ring deposition extended from 7 to 30 April. Hence, these fish could all be attributed to the same spring spawning period as those from the south shore of Long Island.

However, YOY bluefish from the smaller (10–14 cm) size class caught on 23 September in the Hudson River (Fig. 6) were also aged and their back-calculated dates of first ring deposition were found to be predominantly in June and July, and to a lesser extent in May (Fig. 8c). These dates differed greatly from those of fish captured earlier in the year in the Hudson River, and along the south shore of Long Island.

The relationship of ring number and fork length for each year was best described by the following equations: $Y = 132.308X - 29.890$ in 1985 and $Y = 95.532X + 1.186$ in 1986, where X is log fork length and Y is the number of rings (Fig. 9). The slopes of these regressions differed significantly (ANCOVA, $P < 0.001$). Total otolith length and fork length were highly correlated ($r > 0.99$) and increased isometrically. Total otolith length and ring number also had a high correlation ($r = 0.91$).

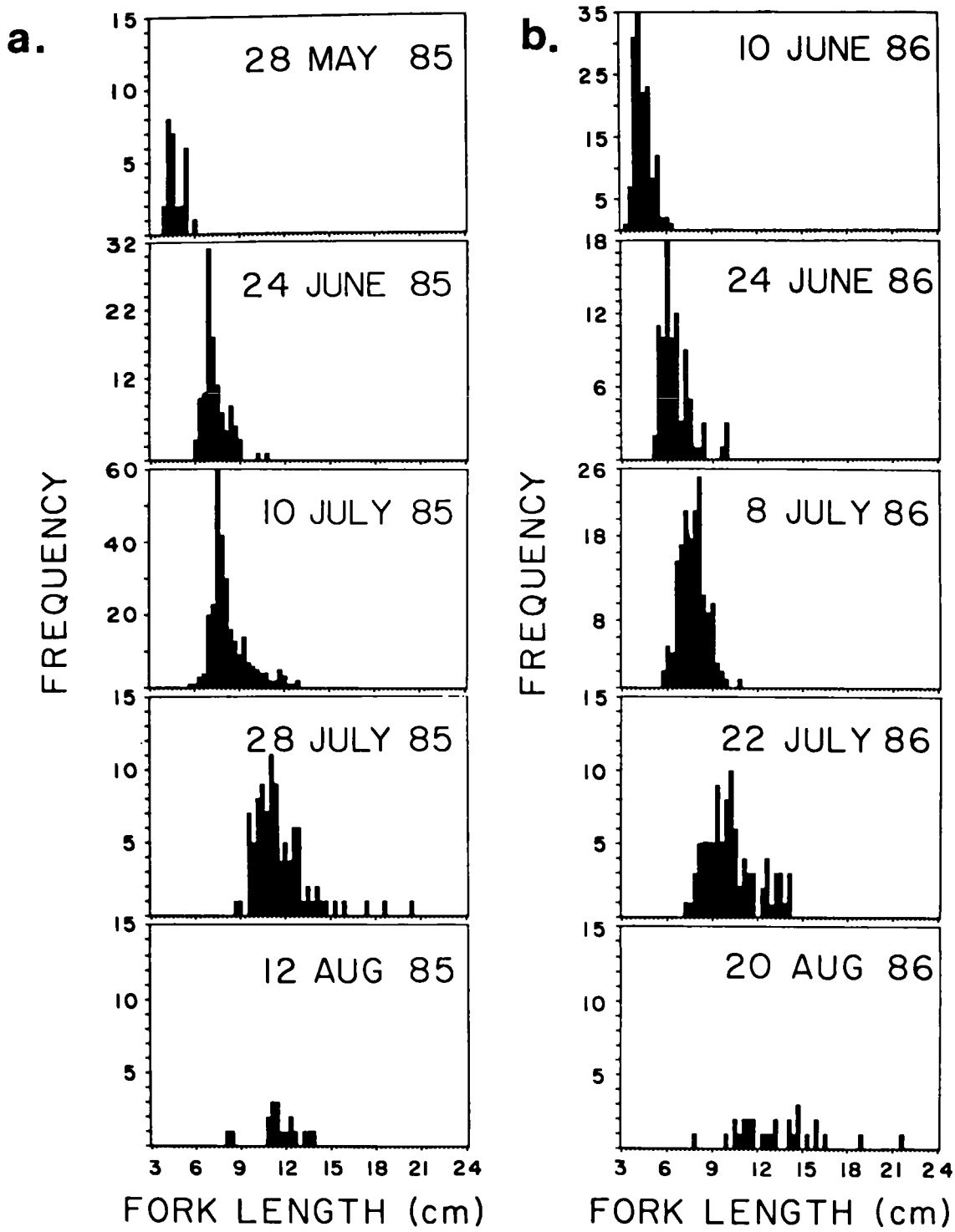


FIGURE 3.—Length-frequency histograms for YOY bluefish (no.) from Great South Bay, NY. (a) 1985; (b) 1986.

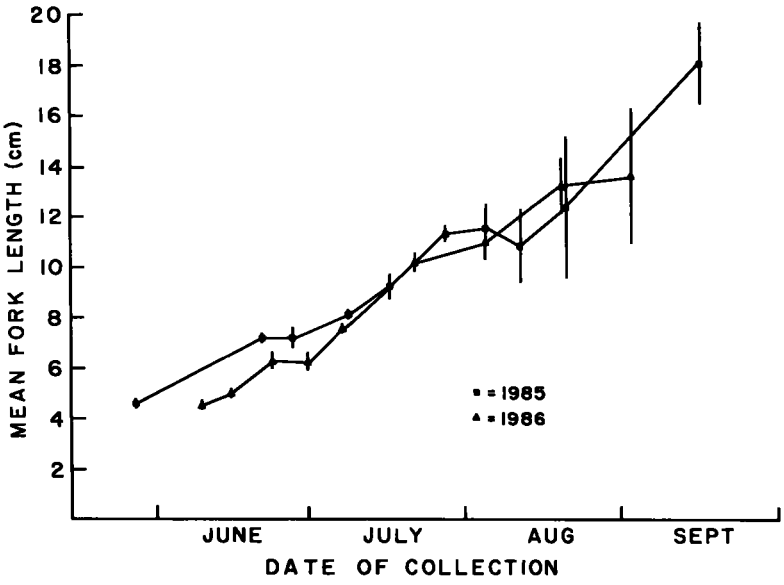


FIGURE 4.—Mean fork length (cm) of YOY bluefish (no.) captured with a beach seine in Great South Bay in 1985 and 1986. Vertical bars are 95% confidence intervals. The last sample in 1986 was caught by angling.

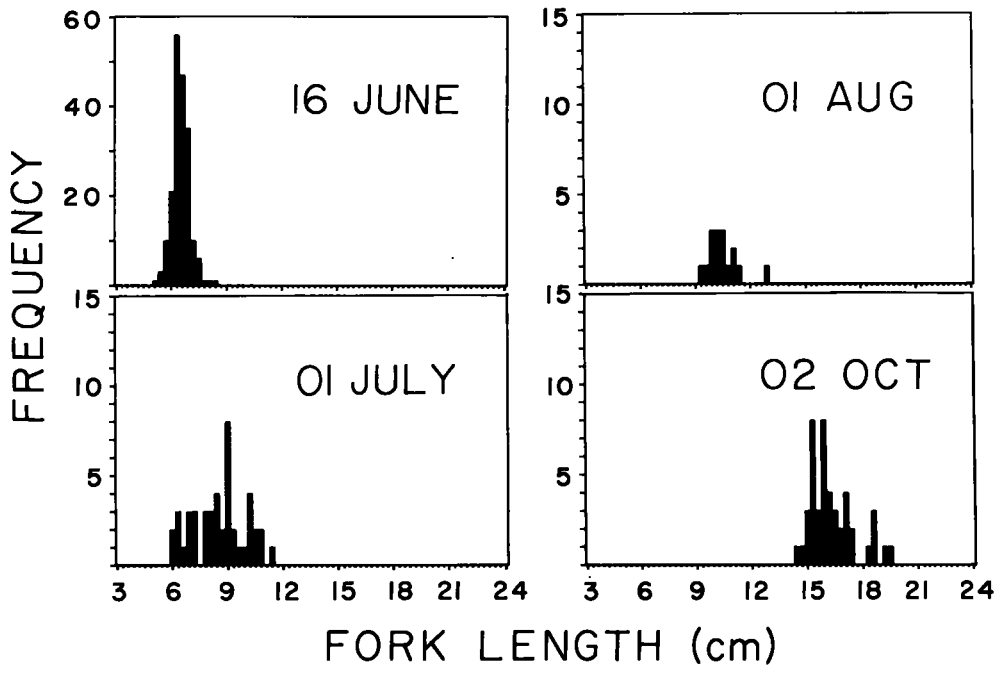
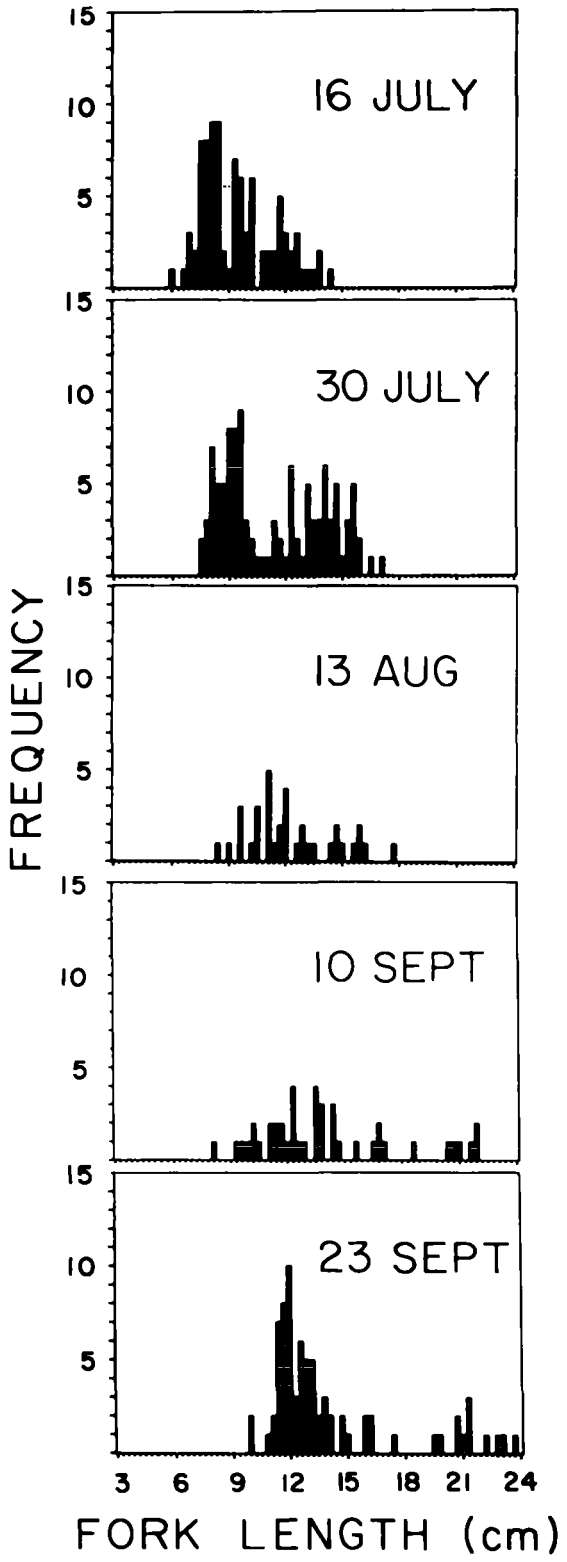


FIGURE 5.—Length-frequency distributions for YOY bluefish (no.) from Jamaica Bay, NY, 1986.



The analysis was then expanded to the remaining samples of YOY bluefish from Great South Bay that had not been aged. The above length-age equations were used to estimate date of first ring deposition from the dates of capture for all YOY captured in each year of sampling from Great South Bay. This exercise revealed that the vast majority of YOY bluefish in our collections from Long Island had dates of first ring deposition in late March, April, and early May (Fig. 10). The weighted mean date of first ring deposition was 8 April 1985 and 14 April 1986.

The age-length equations for YOY bluefish from Great South Bay were not applied to collections from Jamaica Bay or the Hudson River. Preliminary analyses suggested that the age-length equation for fish from the Hudson River differs substantially from those in Great South Bay, probably owing to a difference in growth rate. Geographic variation in the pattern of recruitment and in the age-length relationships of YOY bluefish are being further investigated.

DISCUSSION

Recruitment of YOY Bluefish to New York

In both 1985 and 1986, the arrival of YOY bluefish on the south shore of Long Island was abrupt. Within about a 1-wk period, CPUE went from 0.0 to 14–18 fish/seine haul. CPUE then remained high for the next two months until declining in August and September when the fish probably became too large to be efficiently sampled by our techniques. These data suggest that the YOY bluefish recruit to the shore zone as a sudden pulse. The timing of this recruitment event is apparently variable, differing by about two weeks among the two years of our study. The appearance of fish 3–6 weeks earlier on the south shore (Great South Bay) than on the north shore (Setauket Harbor) of Long Island suggested that these fish arrive from offshore waters to the south.

Temperature probably influenced the time of arrival of YOY bluefish in the shore zone. In both years of our study, YOY bluefish appeared as temperatures reached about 20°–24°C. In October, after temperatures dropped to the middle

FIGURE 6.—Length-frequency distributions for YOY bluefish (no.) from the Hudson River, NY, 1986.

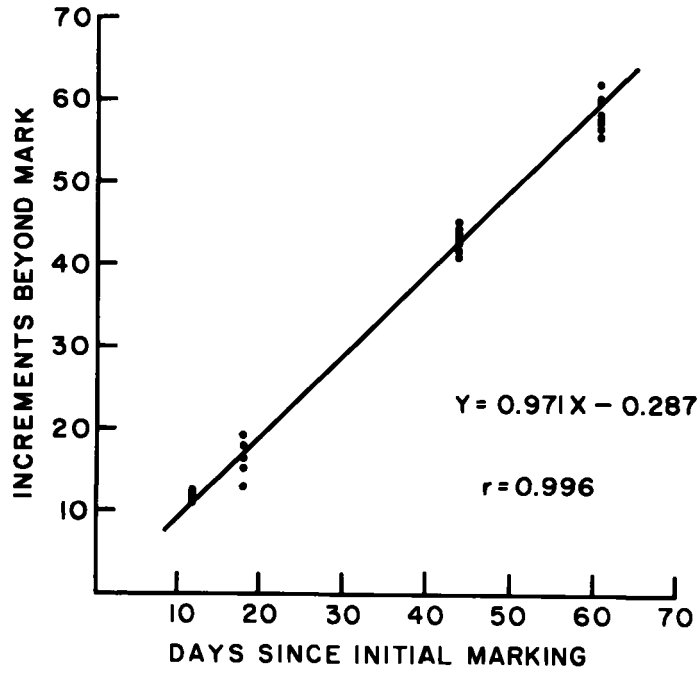


FIGURE 7.—Relation between number of days since marking with tetracycline and the number of growth increments beyond the mark in YOY bluefish maintained in a field cage.

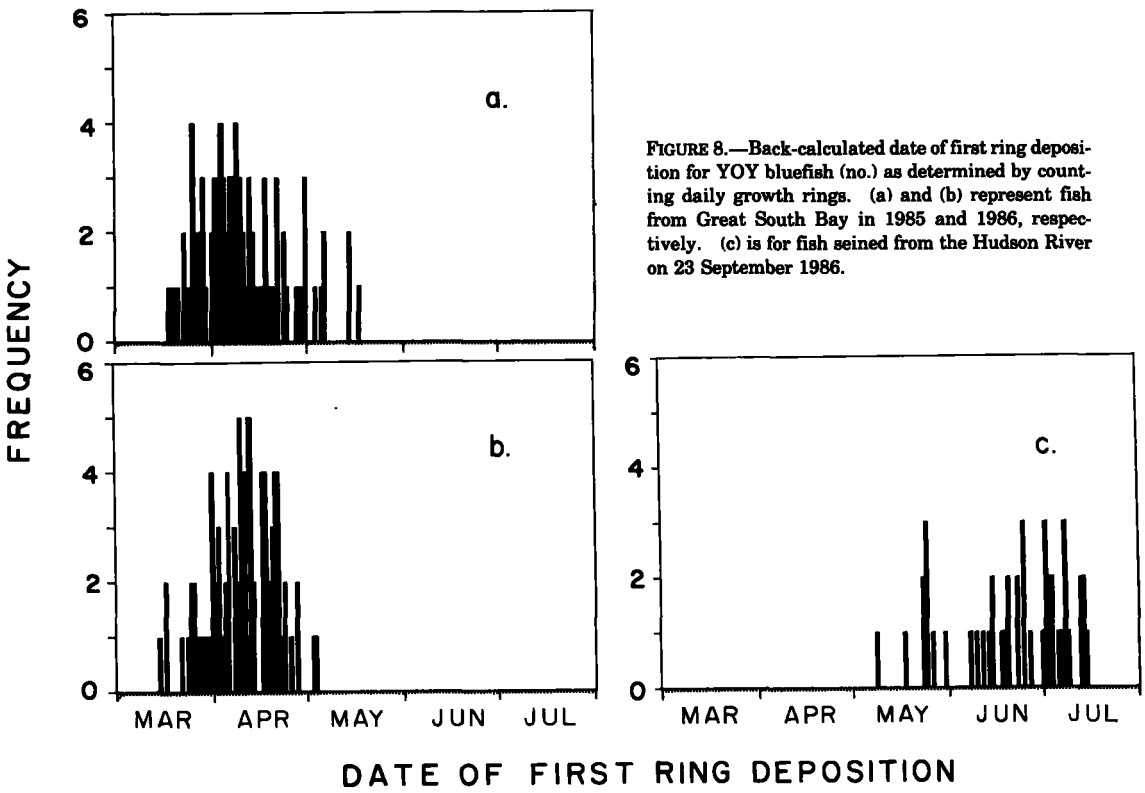


FIGURE 8.—Back-calculated date of first ring deposition for YOY bluefish (no.) as determined by counting daily growth rings. (a) and (b) represent fish from Great South Bay in 1985 and 1986, respectively. (c) is for fish seined from the Hudson River on 23 September 1986.

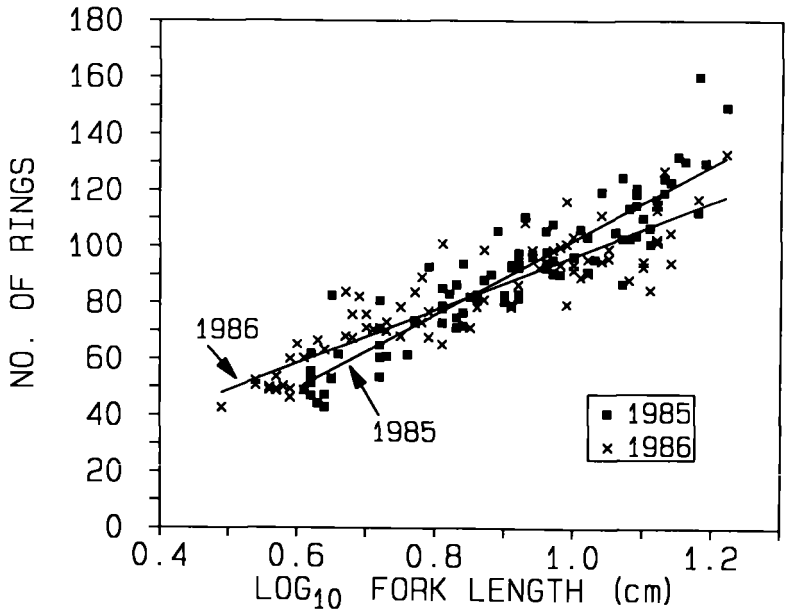


FIGURE 9.—Relation between log fork length (X) and number of otolith rings (Y) for YOY bluefish from Great South Bay, NY. The regression equations are $Y = 132.308X - 29.890$ ($n = 88$) for 1985 and $Y = 95.532X + 1.186$ ($n = 81$) in 1986.

teens, we no longer captured YOY bluefish. Oben (1957) noted that in the Black Sea, YOY bluefish appeared in the shore zone at temperatures of 18°–24.5°C, and left the shore zone in October and November when temperatures dropped to 13°–15°C.

Length-frequency distributions of YOY bluefish from the south shore samples showed only a single mode that attained progressively larger size through the summer and fall, and corresponded to the initial recruitment of fish. If multiple spawning and recruitment events contributed YOY bluefish to Long Island, multimodal length-frequency distributions should have been observed. The unimodal distributions suggested that only one spawning period contributed the majority of YOY bluefish to Long Island.

Interannual variation in the length-age relationship of YOY bluefish was observed. Although recruitment occurred two weeks earlier in 1985 than in 1986, the empirical mean lengths at recruitment were similar (Fig. 4). Postrecruitment growth, however, was slower in 1985 than 1986 so that empirical mean lengths became similar by mid-July. Correspondingly, the slope of the length-age regressions differed significantly among years: YOY bluefish at an age of about 50–70 days had greater fork lengths in 1985 than in 1986 (Fig. 9), but the reverse was true among older, larger fish. Apparently, the growth rate of YOY bluefish prior to recruitment was higher in 1985 than 1986, but this pattern among the two years was reversed during the period of postrecruitment growth.

Validation of Daily Otolith Rings

Our experimental results demonstrate that otolith ring deposition is daily in YOY bluefish. A regression slope of 0.971 indicates a one-to-one correspondence between number of days after injection and the number of rings beyond the tetracycline mark. This outcome is not particularly surprising because numerous studies have shown that increment production is daily, particularly in the early life history when somatic growth is rapid (Brothers et al. 1976; Campana and Neilson 1985; Jones 1985). Cases where ring periodicity is reportedly less-than-daily have involved suboptimal growing conditions (Geffen 1982, 1987; Rice et al. 1985). In our study, the confinement of YOY bluefish in a field cage apparently had little effect on growth rate, or the production of daily growth increments. The field cage allowed for natural light, temperature, and salinity variations that the fish would normally have experienced in na-

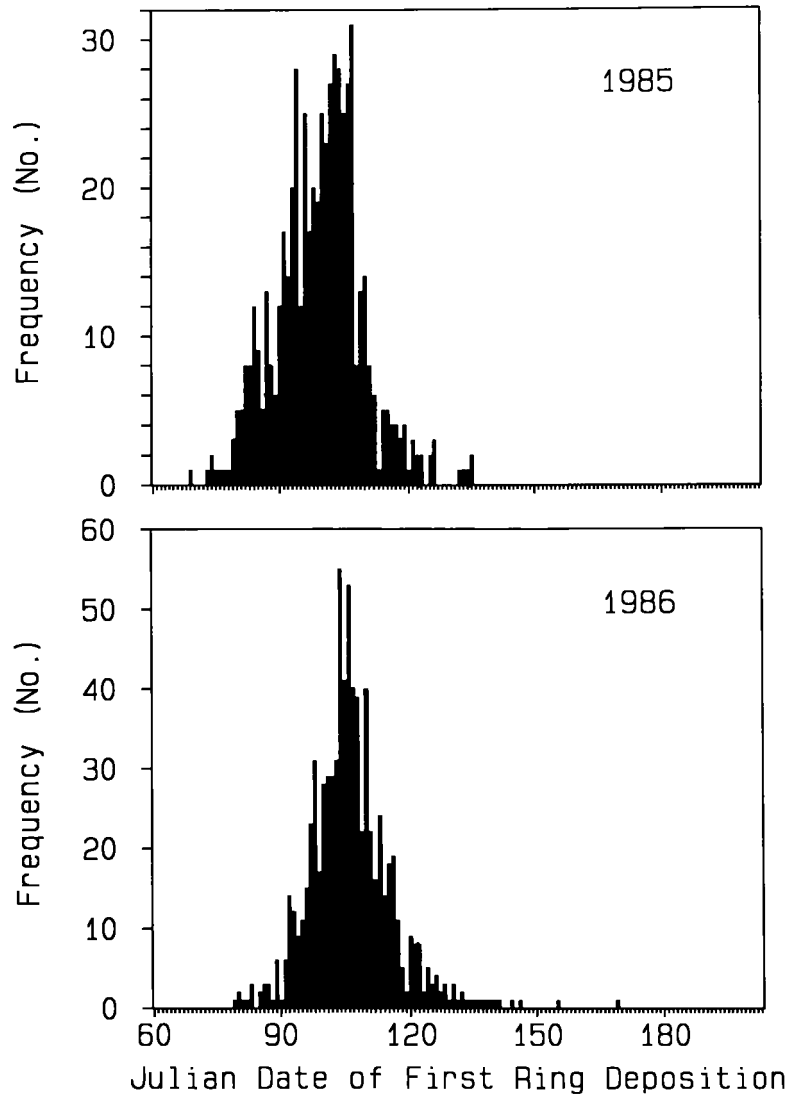


FIGURE 10.—Estimated date of first ring deposition for all YOY bluefish caught in Great South Bay in 1985 (n = 561) and in 1986 (n = 868) using the respective age-length equations in Fig. 9.

ture. Feeding periodicity was probably the primary artifact of confinement that could have affected the rate of ring production in caged fish. However, Marshall and Parker (1982) showed that feeding periodicity did not significantly affect ring production in sockeye salmon, *Oncorhynchus nerka*.

We were unable to determine directly the number of days between spawning and first ring deposition because numerous attempts to capture running-ripe females for initiating experiments on eggs and larvae were unsuccessful. However, most species of fish deposit the first daily growth increment within a few days of hatching (Brothers et al. 1976; Radtke and Dean 1982; McGurk 1984; Radtke 1984; Davis et al. 1985). Recent evidence suggests this is also true in bluefish. Larvae captured off Long Island in 1987 had about seven otolith increments at a total body length of 4–5 mm (R. K. Cowen and D. O. Conover, unpubl. data). Based on the rate of development at 20°C in the laboratory observed by Deuel et al. (1966),

larvae would reach this size in about 5–7 days posthatch. If so, first ring deposition would roughly coincide with hatching. Bluefish hatch in 48 hours at 20°C (Deuel et al. 1966), so the day of first ring deposition probably follows the date of spawning by about 2–4 days.

Spawning Seasons Along the Atlantic Coast

Published studies of larval bluefish distributions along the Atlantic coast suggest the existence of three temporally and spatially distinct spawning seasons: spring and fall spawning seasons in the South Atlantic Bight and a midsummer spawning in the Middle Atlantic Bight. In the only synoptic study covering most of the U.S. east coast, Kendall and Walford (1979) described two periods of high larval abundance: One peak occurred in March and April on the outer shelf of the South Atlantic Bight, and the other peak was in July and August midway over the continental shelf of the Middle Atlantic Bight. Subsequently, Powles (1981) and Collins and Stender (1987) also found the highest abundance of bluefish larvae in the South Atlantic Bight (Cape Canaveral to Cape Fear) to be in April and May. Collins and Stender, however, noted the existence of a lesser peak in larval abundance during September–November. This fall spawning season in the South Atlantic Bight was further confirmed by Finucane and Collins (in press) based on the gonad condition of bluefish from Georgia and the Carolinas. In the Middle Atlantic Bight off Virginia, Norcross et al. (1974) found that eggs and larvae of bluefish first appeared in June, peaked in abundance in July, and persisted into August. Similar observations on the timing of the summer spawning season in the Middle Atlantic Bight were presented by Sherman et al. (1984) and Morse et al. (1987).

Lassiter (1962) provided additional evidence of the existence of relatively discrete spawning seasons in bluefish. He showed that the distribution of back-calculated lengths at age one has a distinctly bimodal pattern among adult fish from North Carolina. Size at age 1 tended to be either about 14 cm or 28 cm. Lassiter showed that the bimodal pattern could not be explained as a difference in growth rate, and suggested that there must be two distinct spawning seasons such that one group of fish had a first growing season about twice as long as the other.

Spawn Dates of YOY Bluefish from New York

Back-calculation to the day of first ring deposition for YOY bluefish recruiting to Great South Bay in 1985 and 1986 demonstrated that these fish were spawned primarily in March and April (Figs. 8, 10). Fish that were spawned in July–August were rarely captured by us on Long Island in 1985 or 1986, despite continued sampling into October.

Recruitment to Jamaica Bay and the Hudson River in July and August 1986 involved YOY bluefish of about the same size as those from Great South Bay. Though the size range of fish from the Hudson was slightly greater than those from Long Island, fish aged from each of the two modes appearing in the July Hudson River samples (Fig. 6) were all spawned during April within about three weeks of each other. The apparent bimodality in July is probably a sampling artifact. Hence, Jamaica Bay and Hudson River fish collected in July and August can be attributed to the same spawning season as those from Great South Bay.

Length-frequency distributions from the Hudson River in September, however, contained a group of unusually small bluefish, and back-calculation showed that they were spawned predominately in June and July (Fig. 8c). These fish probably resulted from the summer spawning season in the Middle Atlantic Bight. Examination of gonads from adult fish captured during 1986 suggested that the running-ripe males and mature females were most abundant during late June and July off Long Island (L. Chiarella and D. O. Conover, unpubl. data). Hence, at least, some summer-spawned YOY bluefish do recruit to the shore zone of the Middle Atlantic Bight. They were, however, much less abundant than spring-spawned YOY bluefish in our 1985 or 1986 samples.

Spawning by bluefish in the spring is known to occur only in the South Atlantic Bight (Kendall and Walford 1979; Collins and Stender 1987). Water temperatures over the shelf north of Cape Hatteras are probably too low for bluefish to spawn in March and April: average shelf water temperatures in the Middle Atlantic Bight range from 5° to 14°C in March and April (Ingham 1986). Virtually no eggs and larvae (Morse et al. 1987) and comparatively few adult bluefish (Gilmore 1985) are captured in plankton or trawl surveys north of Cape Hatteras in March and

April. Moreover, the time of arrival of YOY bluefish on Long Island actually precedes the summer spawning season in the Middle Atlantic Bight. We therefore conclude that YOY bluefish recruiting to the Middle Atlantic Bight in late spring come from spawnings in the South Atlantic Bight.

Larval Transport

The physical mechanisms that account for the transport of bluefish larvae from the South Atlantic Bight to New York are not clear. Spawning in the South Atlantic Bight occurs primarily over the outer half of the continental shelf (Powles 1981; Collins and Stender 1987), and some larvae may be entrained by the Gulf Stream and carried northward into the slope waters of the Middle Atlantic Bight (Kendall and Walford 1979). Neuston net collections in April have shown that bluefish larvae are periodically abundant on both sides of the Gulf Stream-shelf water interface off Cape Hatteras (Kendall and Walford 1979). Collins and Stender (1987) found a negative correlation between larval size and latitude in the South Atlantic, but their sampling may not have extended far enough north (i.e., they did not sample above Cape Fear).

If the Gulf Stream is responsible for the northward transport, a mechanism by which larvae avoid being advected too far offshore would appear to be necessary. According to our results, the interval between spawning and recruitment to Long Island is about 45–60 days, whereas the surface flow of the Gulf Stream at lat. 36°N is about 104 km/day (Iselin 1936). Hence, larvae remaining in the Gulf Stream for an extended period would be transported far off the shelf. Retention near the shelf could be achieved by entering the slope waters at an appropriate time.

The abrupt appearance of YOY bluefish in the shore zone suggests that the onshore migration is a temporally distinct event, perhaps triggered by vernal warming of the shelf. Because the circulation of the slope and shelf waters of the Middle Atlantic Bight is toward the southwest (Sherman et al. 1984), the cross-shelf migration must to some extent involve active swimming.

Very few summer-spawned YOY bluefish were captured in our study. This may not be surprising, however, because the prevailing currents over the midshelf off Long Island would carry larvae to the southwest. If so, summer-spawned fish would be found along the coast from approximately New Jersey to Cape Hatteras. We caution, however, against any general conclusion concerning the lack of summer-spawned fish in New York. There could, for example, be substantial year-to-year variation in the recruitment level of spring- and summer-spawned fish along any particular segment of the U.S. coast. These issues are now being examined by extending our sampling to southern latitudes.

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ON THE ROLE OF FOOD-SEEKING IN THE SUPRABENTHIC HABIT OF LARVAL WHITE CROAKER, *GENYONEMUS LINEATUS* (PISCES: SCIAENIDAE)

A. E. JAHN, D. M. GADOMSKI, AND M. L. SOWBY[1]

ABSTRACT

Fish larvae and their prey were sampled from discrete depths within the bottom meter and at middepth near the 15 m depth contour off southern California. The smallest white croaker larvae (<2.7 mm NL) occurred mostly at middepth. Mid-sized larvae (2.7 mm to the beginning of flexion) were almost all collected at the two depths nearest the bottom. All preflexion-stage larvae ate small (50–300 μm in length) prey, chiefly rotifers, copepod nauplii, tintinnids, and invertebrate eggs. Although small and mid-size larvae ate these items in different proportions, this difference could not be ascribed to vertical distribution. Diet of the largest larvae, flexion and postflexion (roughly 5–15 mm), consisted mainly of copepods and differed by >90% from diets of smaller larvae. Though largest larvae were only captured 50 cm above the bottom, their prey, with one exception (amphipods), were more abundant at or above 1 m. It was concluded that the observed suprabenthic concentration of older white croaker larvae was probably not motivated by food-seeking.

Disparity between concentrations of food required for survival and growth of laboratory-reared fish larvae and observations of average concentrations of food organisms in the ocean has led to the widely accepted idea that aggregations of fish larvae and their food must frequently overlap in nature (see reviews by Theilacker and Dorsey [1980] and Hunter [1981]). Direct and indirect evidence for the importance of overlapping concentrations of larvae and their prey (Lasker 1975, 1978; Govoni et al. 1985; Buckley and Lough 1987) comes from sampling at fronts and discontinuities in the pelagic environment. One interface that attracts many zooplankters is the seabed itself (Hamner and Carleton 1979; Wishner 1980; Sainte-Marie and Brunel 1985). On the southern California continental shelf, the seabed serves as a surface of aggregation for larvae of numerous fish species (Brewer et al. 1981; Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986) and other zooplankton (Clutter 1969; Barnett and Jahn 1987) and of large-zooplankton biomass (Jahn and Lavenberg 1986). While it is tempting to suggest a trophic advantage to the suprabenthic habit of the fish larvae, near-bottom concentrations of organisms actually eaten by larval fishes have yet to be demonstrated along the open coast.

In all cases reported, concentration in the near-bottom zone was greater in older larvae and, when observations permitted, greater during the day than at night (Brewer and Kleppel 1986; Jahn and Lavenberg 1986). The phenomenon is therefore thought to be behavioral. Possible advantages of such behavior, including avoidance of midwater predators, maintenance of position on the shelf, and increased encounters with high concentrations of food, have been discussed elsewhere (Barnett et al. 1984; Brewer et al. 1984; Brewer and Kleppel 1986; Jahn and Lavenberg 1986). In discussing the near-bottom schooling behavior of a larval clupeoid in Japan, Leis (1986) stated, "knowledge of the biology of epibenthic fish larvae is too rudimentary to allow a clear assessment of the advantages and disadvantages. . . ." Whatever the advantages, a seemingly more answerable question about the near-bottom habit is what causes the larvae to behave as they do? In another study from Japan, Tanaka (1985) showed that juvenile red sea bream, *Pagrus major*, exploited suprabenthic copepod populations, and he speculated that the distribution of prey was a template for the descent of the fish from midwaters and its subsequent migration into estuaries. The question addressed in the present study was whether the fine-scale layering of larval fishes was a direct response to that of their prey field.

Because of the immediate behavioral aspect of

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the question posed, a 1-d study was thought appropriate. Though environmental conditions on this day might differ from "average", fish larvae were assumed to be capable of a constant array of behaviors. In other words, response (if any) of the larvae to the vertical distribution of their prey was assumed to be a deterministic rather than a statistical phenomenon. If their vertical distribution resembled that of their prey, then food-seeking would remain a plausible explanation for the near-bottom habit; if not, then other stimuli must be considered important in shaping these near-bottom concentrations of fish larvae.

The sampling was planned for daylight hours, when most feeding by larvae was expected to occur (Hunter 1981; Govoni et al. 1983). Late winter was chosen because in this season peak larval abundances of several species of interest to us (northern anchovy, *Engraulis mordax*; white croaker, *Genyonemus lineatus*; California halibut, *Paralichthys californicus*; and sometimes queenfish, *Seriphus politus*, often overlap (Lavenberg et al. 1986). A survey cruise in late February found moderate-to-high abundance of the first three species plus California sardine, *Sardinops sagax*, (all >0.2 m^{-3}, Lavenberg unpubl. data), and so this study was scheduled for 19 March 1985 off Seal Beach, CA (lat. 33°41'N, long. 118°05'W; for a map, see Jahn and Lavenberg 1986).

As it happened, we chanced to encounter conditions that were less typical than those found on the February cruise. Only one fish species, white croaker, was abundant enough to merit analysis, and an uncommonly reported prey item, rotifera, was important for small larvae. The diet of various-sized larvae with respect to the abundance of prey organisms at an array of heights above the seabed was nevertheless useful in questioning whether food-seeking shaped the observed larval distribution.

METHODS

Field

At the hour of 0750 PST, an array of Interocean model S4[2] electromagnetic current meters was set out over the 15 m isobath, with current meters 1, 4, and 8 m above the seabed. These meters were set to record average current vectors and temperature at 5-min intervals. The vessel (RV *Westwind*) was then anchored some 200 m seaward of the current meter array. A Nielson model NCH fish pump, rated at 227 m^3 h^{-1} at a 2 m head, was used to sample fish larvae and zooplankton. The end of the hose was tethered between a 200 kg flat steel weight and several subsurface floats, with a pulley arrangement such that divers could adjust the distance between hose mouth and seabed. A similar setup was previously found to give repeatable, fine-scale resolution at vertical separations of 25 cm (Jahn and Lavenberg 1986). Sampling heights above the bottom were 50 cm, 1 m, and 6.7 m. The 15.2 cm diameter hose was nearly horizontal at the tether point, so that nominal sampling strata were $z \pm 7.6$ cm. Vessel surge, transmitted through the stiff hose, caused occasional downward excursions of some 10 cm.

Accompanying each pump sample was a cast of water bottles for phytoplankton and microplankton analysis. Rigid arrays of horizontally held 4 L Niskin bottles (cf. Owen 1981) were used to take water samples simultaneously from 25, 50, and 100 cm above the bottom. The bottle array was designed to be tripped by messenger, but poor performance led to diver-implemented use after the second cast. A midwater sample, 7.5 m below the surface, was obtained via a single Niskin bottle for each sample set.

The sampling plan thus consisted of duplicate pump samples from each of three strata, each pump sample to be accompanied by a set of bottle samples from four standard heights, three within 1 m of the seabed and one at midwater column. One-liter samples from the bottles were fixed in Lugol's solution for later identification of phytoplankton and microplankton. Pump samples of 15-min duration (approximately 35 m^3) were mainly directed into an overboard, 330 μm mesh plankton net for retention of large zooplankton and ichthyoplankton. Unexpected problems in reading an inline flowmeter required that volumes be estimated as 2.4 m^3 min^{-1}, based on previous experience with the pump under similar conditions aboard the same vessel. To collect smaller zooplankton, a 5 cm diameter hose led from the intake side of the fish pump to a 100 μm mesh plankton net. This small-meshed net was suspended over a watertight box, which was marked such that exactly 0.5 m^3 could be subsampled for animals too small to be quantitatively retained by the large net. This subsample, which

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

was first seived through 330 μm mesh, took about 10 minutes to obtain; the portion retained on the 330 μm mesh was added to the contents of the large plankton net. All pump samples were preserved in 5% formalin.

Laboratory

All fish larvae and eggs were sorted from the large zooplankton samples and identified. All specimens of white croaker, the only species abundant in all six collections, were measured with an eyepiece micrometer in units of 0.024, 0.062, or 0.159 mm, depending on magnification. Length was measured from tip of snout to end of straight (NL) or flexed (FL) notochord or to the end of the hypural plate when this margin was vertical (SL). A further designation of developmental stage indicated the amount of yolk present: "free embryos" (Balon 1975) had a relatively massive yolk sac and may or may not have had functional eyes and mouths; more advanced individuals with a much-reduced or totally resorbed yolk sac, fully pigmented eyes, and an apparently functional mouth were designated "feeding-stage" larvae, or simply "larvae".

All larvae, plus a maximum of 20 free embryos with apparently functional mouths from each collection, were dissected for gut contents analysis by methods described in Arthur (1976) and Gadomski and Boehlert (1984). Length, rather than width, of prey items was measured, because it was considered a more conservative property of often crushed specimens and because our concern was not so much with what the larvae *could* eat (Hunter 1981) as with what they *did* eat. Lengths of prey items (of copepods, cephalothorax length) were recorded in 50 μm classes up to 200 μm, by 100 μm classes from 200 μm to 1 mm, and by 0.5 mm classes at larger sizes. In a few cases, these size categories were inconvenient, and more inclusive ranges were used.

Water bottle samples of phytoplankton and microzooplankton were prepared following procedures in Utermöhl (1931). From a thoroughly agitated sample, a 50 mL subsample for net phytoplankton was taken and placed in a settling chamber overnight (about 14–18 hours). Cells were identified and counted in 10 ocular fields, and mean density (cells per liter) calculated as the number counted scaled by the proportion of the area of the 10 fields (20.6 mm^2 total) to the area of the slide (510.7 mm^2).

Microzooplankton was filtered from a 500 mL subsample onto a 35 μm mesh screen, washed from the screen into a 50 mL settling tube and allowed to settle overnight. All organisms >50 μm were counted and identified to taxon and size category, using the same system as for larval fish gut contents. Densities were scaled to number per liter.

The 100 μm zooplankton samples were concentrated to 200 mL, then subsampled twice using a 10 mL Stempel pipette. Organisms were identified and classified to size categories as described above for larval fish prey. Counts from two subsamples were averaged and expressed as number per m^3.

Data Analysis

The microzooplankton (from water bottles) data set consisted of six vertical profiles of four sampling heights each. Principal components analysis was used to look for vertical layering and time-correlated changes in the makeup of these assemblages. A list of taxa present in three or more samples from at least one sampling height was chosen. Abundances were log-transformed $[\log_{10}(x + 1)]$, and principal components computed from the covariance matrix. Component scores for each of the 24 samples were used to make plots in which two- and three-dimensional groupings were sought that could be clearly related to sampling height or to the sequence in which the samples were taken. The taxa having high loadings on axes (components) identified with time and vertical trends were subsequently scrutinized individually. A similar analysis was done for phytoplankton, but omitted here in the interest of brevity.

Gut contents were conveniently analyzed by lumping taxa into the 10 categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, invertebrate egg, and "other". Unidentifiable matter was ignored in all comparisons. To test for differences in diet between subsets of larvae, we used an adaptation of the "bootstrap" (Efron 1982). The test criterion was the percentage of prey comprised by a major item in one of the two groups of guts. The null hypothesis that two sets were not different was simulated by combining the two data sets and then, through repeated sampling, determining the probability of observing the criterion percentage from such a mixture.

RESULTS

General Observations

The water column was very weakly stratified, with temperatures of 12.9 ± 0.1°C at 1 m, 13.0 ± 0.2°C at 4 m and 14.1 ± 0.1°C 8 m above the bottom during the time of biological sampling. Near the bottom, a turbid suspension limited visibility to arm's length; the surface of the sediment was never clearly seen on any of the seven descents during the hours of 0930–1630. The midwaters below about 3 m from the surface were densely populated with larvaceans (visually estimated and later confirmed to be about 10 L^{-1}). Total diatom cell counts (principally *Nitzschia* spp.) were of order 10^5 L^{-1} in all samples, bloom quantities suggestive of recent upwelling (cf. Tont 1981).

Currents and Plankton

During the hours of biological sampling, currents ran steadily alongshore to the southeast, being deflected counterclockwise near the bottom and ranging from about 14 cm s^{-1} at 8 m to 6 m s^{-1} at 1 m above the seabed. At these current speeds, one may expect that the approximately 5-h period from beginning to end of biological sampling should correspond to a minimum spatial spread of 1–2.5 km. Distances of this order were previously found to be an important length scale of variation in larval fish abundance (Jahn and Lavenberg 1986). Because the spatial dimension of interest regarding distribution of larval fish prey was the vertical, we needed to quantify, at least partially, the effects of time (vertical migration?) and distance (advection) on the composition and vertical dispostion of the plankton.

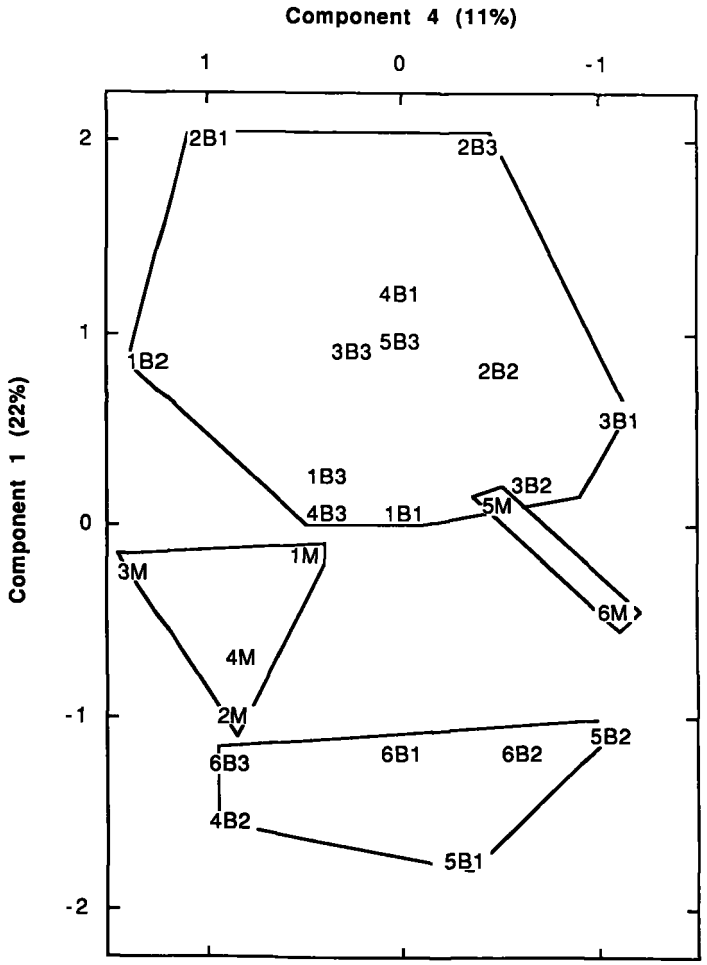

FIGURE 1.—Projections of microzooplankton samples onto the first and fourth principal component axes. The initial digit represents profile number, M = midwater, B = near-bottom, final digit is proximity to bottom (1 = 25 cm, 2 = 50 cm, 3 = 100 cm), see Figure 3.

Accordingly, the microplankton data set, representing six vertical profiles separated in time, was reduced to principal components for examination of possible time effects.

Twenty-four taxonomic/size categories of microzooplankton were used to compute principal component scores for the 24 samples. The first four principal components accounted for 60% of the variance. No clear separation of midwater from near-bottom samples was seen. The first component, which accounted for 22% of the variance, separated the near-bottom samples into two groups, morning to midday and afternoon (Fig. 1), leaving the midwater samples at intermediate projections. The midwater samples were in turn separated by the fourth component (11% of the variance) into time groups corresponding to those of the near-bottom set. No stratification by sampling height was seen within the near-bottom samples, and none of the other axes provided separation by time. The highest loading variables on components 1 and 4 (Table 1) were various sizes of rotifer and, for component 1, three genera of tintinnids (*Favella*, *Acanthocystis*, and *Dadayella*). Much of the time-correlated variance structure depicted in Figure 1 thus appears to be due to change in the size composition of rotifers, described in a later section, and a decrease in these three tintinnids near the bottom in late afternoon (Table 2). An identical analysis of the phytoplankton data found no trends in time or depth.

TABLE 1.—Loadings of important variables on the first and fourth principal components of microplankton data.

Component 1		Component 4	
Variable	Loading	Variable	Loading
Rotifer		Rotifer, 100–150 μm	0.388
150–200 μm	0.572		
200–300 μm	−0.380	Egg, 50–100 μm	0.349
Tintinnids		Copepod nauplii,	
Favella sp.	0.365	150–200 μm	−0.252
Acanthocyctis sp.	0.331		
Dadayella sp.	0.314		

Larval Fish Abundance

Of 1,125 total fish larvae taken in the six pump samples, 666 (59%) were white croaker, a deep-bodied, robust larva (Watson 1982). More than half (338) of these had absorbed the yolk sac and were thus of feeding size. The second most abundant feeding-stage larva was an unidentified gobiid type (84 specimens), but this taxon was not taken above 100 cm of the seabed and so was excluded from the gut analysis. Feeding-stage California sardine, northern anchovy, and California halibut—all relatively abundant (>0.2 m^{-3}) in the area three weeks earlier—each represented <1% of the catch. Although the earlier survey employed oblique bongo net tows, past comparison of the Nielsen pump with bongo tows found no significant differences in diversity or abundance estimates based on similar-volume samples (R. Schlotterbeck[3]). We therefore think the differences between the February survey and our March samples were due mainly to a real change in the ichthyoplankton, from a typical late winter assemblage (McGowen 1987; Walker et al. 1987) to a more depauperate one.

Vertical Distribution and Feeding Incidence of Larval White Croaker

White croaker free embryos ranged in abundance from <0.1 m^{-3} at 0.5 m to ≈1 m^{-3} at 1 m to >2 m^{-3} at 6.7 m above the bottom. Of 61 free embryos dissected, none had gut contents.

Feeding-stage larvae of white croaker were only slightly more abundant at 6.7 m (1.9–2.2 m^{-3}) than at 1 m and 0.5 m (1.1–1.6 m^{-3}), but

[3]R. Schlotterbeck, Robert Schlotterbeck, Inc., 18842 Ridgeview Cr., Villa Park, CA 92667, pers. commun. April 1986.

TABLE 2.—Density (cells per liter) of three tintinnids as a function of time and sampling height. Each set of three numbers gives the density of *Favella* spp. (F), *Acanthocystis* spp. (A), and *Dadayella* spp. (D).

Height	Time (PST)																	
	1030			1130			1220			1313			1425			1454		
(cm)	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D	F	A	D
750	6	4	20	0	4	22	0	4	12	2	0	12	46	12	14	42	6	18
100	2	4	24	30	18	24	6	18	48	0	2	26	8	4	24	0	0	26
50	0	6	18	26	12	44	0	2	24	0	0	4	0	0	4	0	6	12
25	2	6	4	14	12	44	0	22	54	10	2	26	0	0	0	0	0	0

there was a marked gradient in development with proximity to the seabed (Fig. 2). All the larvae at 6.7 m had unflexed notochords, and most were <2.5 mm NL. Feeding incidence (proportion of larvae with nonempty guts) was 78% at this height. At 1 m, modal larval length was 2.65 mm, with a single postflexion specimen (Fig. 2); feeding incidence was 74%. At 0.5 m there were still some preflexion larvae, but a second length mode at 6.8 mm represented postflexion-stage larvae. Feeding incidence was 90% at 0.5 m above the bottom, being somewhat greater among flexion

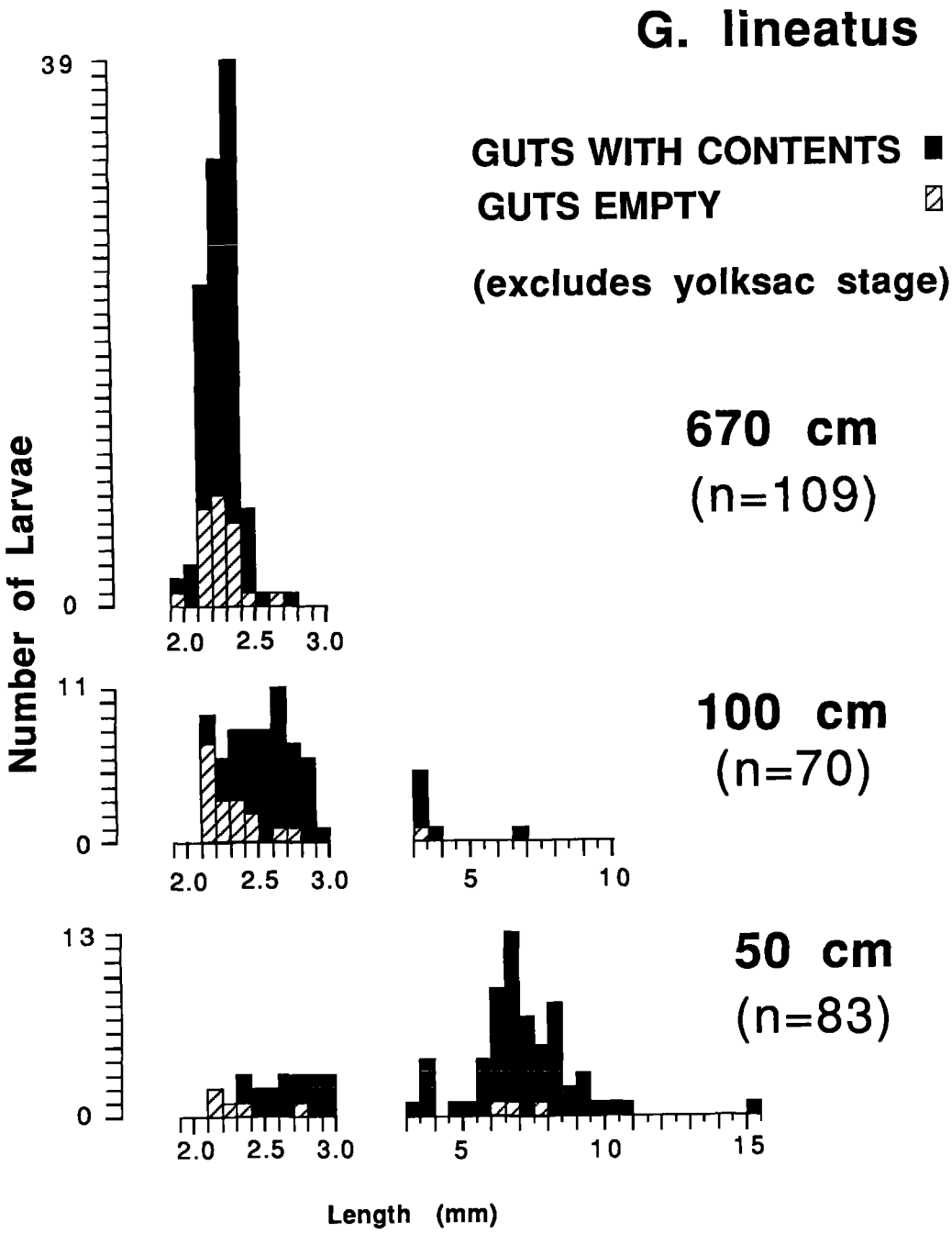

FIGURE 2.—Length frequencies of feeding-stage larvae of *Genyonemus lineatus* at three sampling heights.

and postflexion larvae (95%) than among preflexion larvae (82%).

Gut Contents

The white croaker larvae were divided into three size classes for analysis of gut contents with regard to height above the bottom: preflexion larvae <2.7 mm (size 1), preflexion larvae >2.7 mm (size 2), and flexion and postflexion larvae (size 3). The largest preflexion larva was 4.6 mm NL, and the smallest flexion stage larva was 5.5 mm FL. The division of preflexion larvae at 2.7 mm retained all but one specimen at 6.7 m in size 1 while partitioning the preflexion larvae at 1 m and 0.5 m about equally into sizes 1 and 2 (Figs. 2, 3). Besides the 2.75 mm specimen at 6.7 m, a single flexion stage larva at 1 m was excluded by these criteria from the comparisons.

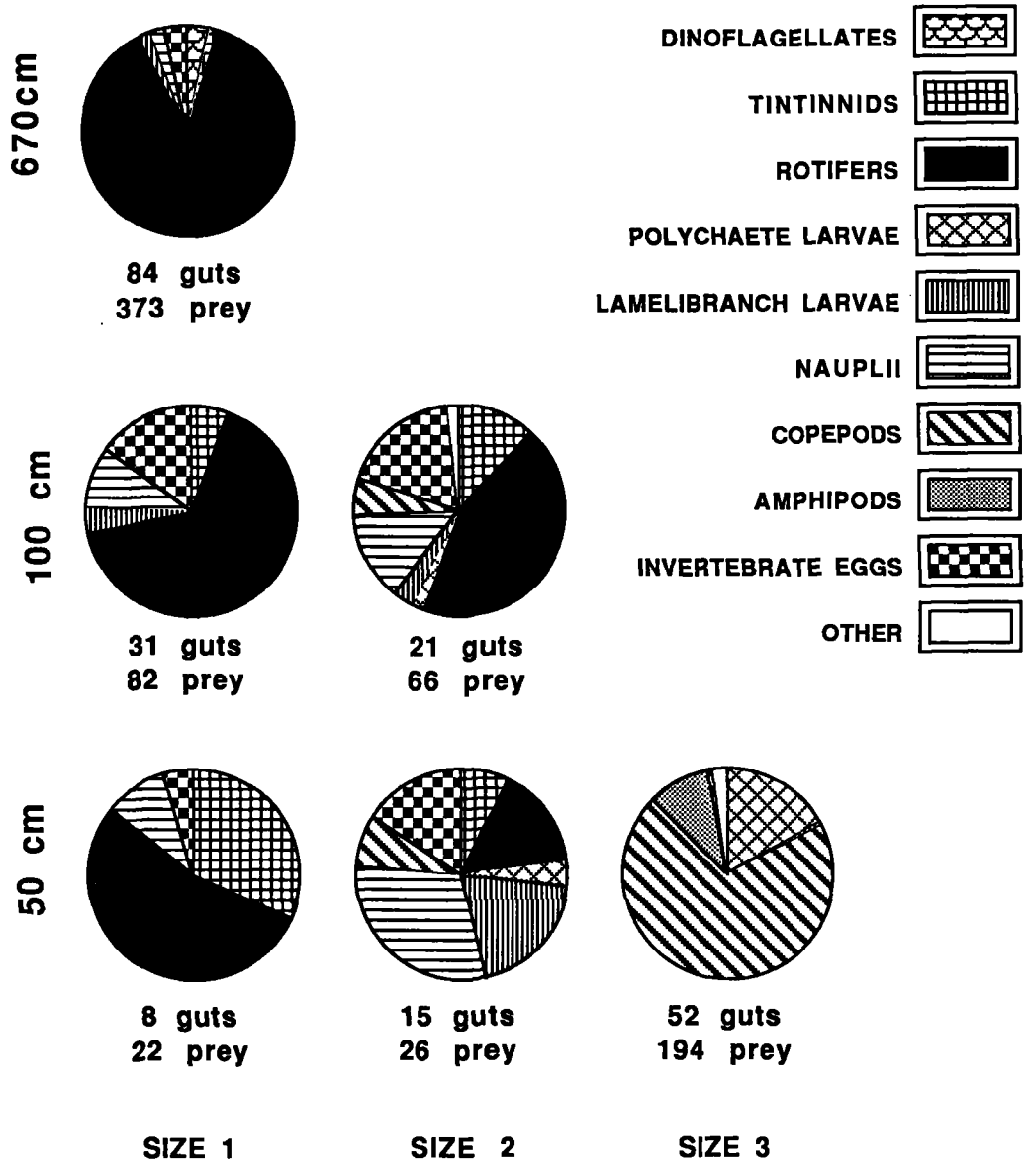

FIGURE 3.—Percentage contribution of 10 food categories to the diet of larval white croaker at three heights above the bottom. Size 1 = preflexion larvae <2.7 mm NL; size 2 = preflexion larvae >2.7 mm NL; size 3 = flexion and postflexion-stage larvae.

Most identifiable prey items fit into the nine categories: dinoflagellate, tintinnid, rotifer, polychaete larva, lamellibranch larva, crustacean nauplius, copepodite and adult copepod, amphipod, and invertebrate egg (Fig. 3). The "other" category applied only to size-2 larvae at 1 m (1 *Globigerina* sp.) and to size-3 larvae (1 zoea, 3 larvaceans, and two large [1 mm] unidentified spheres).

Guts of preflexion (sizes 1 and 2) larvae from the three sampling heights contained an array of small (<300 μm) organisms that varied mainly in proportions from mostly rotifers (88%) in size-1 larvae at 6.7 m to a diverse mix of prey numerically dominated by nauplii in size-2 larvae at 0.5 m (Fig. 3). Percent similarity (overlap) among the 5 groups of preflexion larvae ranged from 24 to 75%. The gut of the single size-2 larva at 6.7 m, not included in Figure 3, contained two tintinnids.

Size-3 larvae had a diet consisting chiefly of copepodite and adult copepods that overlapped only 8–9% with size-2 larvae and 1% or less with the three groups of size-1 larvae. The copepods eaten by size-3 larvae were mostly *Corycaeus anglicus* (62% of all copepods), unidentified copepodites (cyclopoid and calanoid, 25%), and *Paracalanus parvus* (9%). Polychaete larvae were identified only from the presence of setae in the guts, so the proportion (nominally 16% of all prey items) of this taxon in the diet is more an indication of incidence than of numerical importance. Amphipods, mostly in the length range 1–1.5 mm, were found in white croaker larvae ranging from 6.5 mm FL to 10.3 mm SL. The gut of the flexion-stage larva at 1 m, not included in Figure 3, contained three *C. anglicus* and traces of polychaete setae.

While there can be no doubt that flexion and postflexion larvae had a different diet than preflexion larvae, the pattern of decreasing proportion of rotifers with increasing size and proximity to the bottom among preflexion larvae was of questionable statistical significance. The first question asked was whether the very high percentage of rotifers in the diet of size-1 larvae at 6.7 m was likely to have arisen by chance from a random sampling of size-1 larvae. Formally stated, H_0 = "all size-1 larvae had the same percentage of rotifers". The 123 nonempty guts were pooled, and random samples of 84 each were drawn. In 1,000 iterations, <4% of the samples had ≥88% rotifers, so it was concluded that larvae at 6.7 m ate significantly more rotifers than similar-sized larvae near the bottom. The remaining 75 preflexion larvae (sizes 1 and 2) are divided into 4 small groups at 0.5 and 1 m, so we next tested for a size effect by pooling across sampling height, such that the guts of the 39 near-bottom size-1 larvae contained 64% rotifers, and the 36 size-2 larvae had 36% rotifers. Bootstrapping as before, <2% of samples of 36 had ≤36% rotifers, so it was concluded that size-1 and size-2 larvae differed in this regard. Further testing (e.g., of a height effect within sizes) was not done because of small sample sizes and multiple testing considerations.

Abundance and Vertical Distribution of Prey

Rotifers, all identified as the brachionoid *Trichocerca* sp., figured importantly both in the diet of preflexion larvae and in the time-related variance structure of the microplankton. As shown in Table 3, there was a change in the size spectrum of these animals that coincided approximately with the time of changing from near-bottom sampling to midwater sampling with the fish pump. It was only the largest category of rotifer (200–300 μm, including the "toe") that was found in the guts of the larvae. The relative abundance of total rotifers in the plankton at the times and heights of pump sampling differed very little (25–33% of all organisms in the 100–300 μm size class), but the percentage of rotifers in the 200–300 μm class increased from 21% (near-bottom, morning) to 86% of all rotifers (midwater, afternoon). The dominance of rotifers in the diet of size-1 larvae in midwaters is thus likely related to the larger size of rotifer resident in the water column when that height was sampled.

The most notable dietary difference among the larval size groups analyzed was the switch from small (50–300 μm) to larger (0.5–2.5 mm) prey, principally the copepod *Corycaeus anglicus* (0.5–0.8 mm), upon flexion of the notochord. The abundance of *Corycaeus* from the 100 μm mesh pump samples (Table 4) shows that this prey item was equally or more abundant in midwater than near the bottom, where all the flexion and postflexion larvae were captured. (Within the bottom meter, the similar-sized but more transparent *Paracalanus parvus* outnumbered *C. anglicus* by a factor of 5–20.) The only prey found in numbers in these larvae that was restricted to the 0.5 m samples was gammarid amphipods. Larger crustaceans—cumaceans, crab and shrimp zoea,

TABLE 3.—Density (rotifers per liter) of *Trichocerca* sp. as a function of time and sampling height. Each set of three numbers gives the density of 100–150 μm, 150–200 μm, and 200–300 μm rotifers. Height of simultaneous pump sample is given.

Time (PST):	1030			1130			1220		
Pump height:	0.5 m			0.5 m			1 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	8	0	4	4	0	10	0	0	20
100	8	14	0	0	66	0	14	22	10
50	24	18	0	0	8	40	0	34	0
25	0	2	12	16	46	0	0	30	0
Time (PST):	1313			1425			1454		
Pump height:	1 m			6.7 m			6.7 m		
Sampling height (cm)	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm	100–150 μm	150–200 μm	200–300 μm
750	20	0	0	0	12	14	0	0	60
100	0	4	0	12	24	0	46	0	102
50	6	0	34	0	4	16	0	0	42
25	0	26	0	0	0	6	0	2	0

TABLE 4.—Abundance (animals m^{-3}) of copepodite and adult *Corycaeus* spp. in 100 μm mesh samples from the fish pump.

Height (m)	First sample	Second sample
6.7	1,080	460
1	120	500
0.5	180	140

mysids, and euphausid furcilia larvae—were all abundant (>10 m^{-3}) in the 0.5 m, 330 μm mesh samples but with the exception of the *callianassa* zoea mentioned above (from the gut of an 11 mm larva) were not found in these white croaker larvae.

DISCUSSION

The chief drawback of the pumping system used was its inability to obtain a simultaneous vertical profile. The sampling sequence left the possibility that differences among heights might be confounded by trends in time, as discussed by Jahn and Lavenberg (1986). Slight time effects were found among the vertical profiles of microplankton, increasing the suspicion that the apparent vertical distributions of fish larvae and macrozooplanktonic prey might have horizontal components. To contradict the argument that food-seeking did not bring postflexion larvae near the bottom, one would need to invoke either an afternoon increase of some two orders of magnitude in copepod abundance (Table 4) or else the presence of flexion and postflexion larvae throughout the water column in morning and midday followed by their sudden disappearance in the afternoon.

A two-order-of-magnitude change in copepod species abundance over a distance of roughly 1 km (2 hours at 14 cm s^{-1}) is certainly possible; though zooplankton structures reported from the southern California continental shelf are generally larger than this (Star and Mullin 1981; Barnett and Jahn 1987), there is always the possibility of sampling the edge of a patch. Since no such edge was evident in the abundance or overall composition of microplankton or of phytoplankton, it seems unlikely that a macrozooplankton change of this order occurred. Moreover, the main copepod eaten, *Corycaeus anglicus*, is generally more abundant in midwater than near the bottom over the shallow shelf (A. Barnett[4]), in accord with its apparent distribution in this study. As to a possible midwater abundance of postflexion white croaker larvae, no such concentration has ever been reported. In some nine vertical profiles taken in daylight over a 6-d period, Brewer and Kleppel (1986) took virtually all specimens >3.5 mm in their near-bottom sampler. White croaker appears similar to another abundant sciaenid, queenfish, in this regard (cf. Jahn and Lavenberg 1986).

[4]A. Barnett, Marine Ecological Consultants, 531 Encinitas Blvd., Encinitas, CA 92024, pers. commun. July 1987.

The only unequivocal instance in which a prey item of larval white croaker was vertically distributed similarly to the larvae was the trace of amphipods found in the guts of competent (flexion and postflexion) larvae. At the lengths of larvae sampled (<12 mm) the prey were all planktonic and nearly all about equally abundant in midwaters as near the bottom. The small numbers of amphipods eaten may indicate an incipient transition to larger, suprabenthic crustacean prey. The size gap between the large prey of these competent larvae and the smaller prey of preflexion larvae is probably an artifact of the bimodal size distribution of sampled larvae. Though all of the prey eaten by size-1 (<2.7 mm) larvae were <300 μm in length, the more varied diet of larger preflexion larvae contained some copepods as big as 500 μm. There is therefore nothing in these data to suggest that the switch from microplanktonic to macroplanktonic prey is anything but a gradual transition as the larvae grow.

Brewer and Kleppel (1986) also reported a change to copepod prey in white croaker larvae >6 mm. Our findings are further similar to those of Brewer and Kleppel in that there was no indication that food-seeking had anything to do with the descent of larval white croaker from midwaters to the near-bottom zone. The other definable dietary trend in this study (besides ontogenetic change) was the high percentage of rotifers eaten by midwater preflexion larvae. This was apparently related to subtle but important differences in the available planktonic prey—significantly, to a greater abundance of suitable-size rotifers—at the time the midwater stratum was sampled.

It seems safest to conclude that white croaker larvae descend toward the bottom for reasons quite apart from seeking food (see discussions in Barnett et al. [1984], Brewer and Kleppel [1986], Jahn and Lavenberg [1986]) and simply eat whatever they find there that suits them. Many potential macroplanktonic prey also favor the near-bottom layer (Jahn and Lavenberg 1986; Barnett and Jahn 1987). Older larvae and their prey may occupy the near-bottom layer for different reasons, or it may be that a single advantage, or set of pressures, underlies the behavior of these diverse planktonic and semi-planktonic taxa. Some species need to remain near shore, and living in the bottom boundary layer helps assure this. The boundary layer also tends to be more turbid than overlying waters and so may lessen an animal's jeopardy to visual (biting) planktivores. (The generality of the latter explanation only holds if suprabenthic fish larvae are less important planktivores than other water-column inhabitants—see Cushing 1983.)

Rotifers have never to our knowledge been reported as an important food of ocean-caught fish larvae, even though the genus *Brachionus* is commonly cultured for feeding larval fish in the laboratory. Schmitt (1986) reported that small, laboratory-reared larval northern anchovy readily fed upon (unidentified) wild-caught rotifers. Rotifers are only occasionally abundant in neritic waters, and never in oceanic waters (J. Beers[5]). Their rarity notwithstanding, rotifers have the ability very rapidly to dominate marine microplanktonic assemblages (Hernroth 1983), and their good food quality (Theilacker 1987) and high secondary productivity for a period of weeks might constitute a significant enhancement to growth and survival of a larval fish cohort.

Our previous experience in handling larval white croaker specimens agrees with the findings of Brewer and Kleppel (1986) in that lamellibranch larvae, easily seen through the body wall, are a common food for small white croaker larvae. In our study, this taxon was a minor constituent of the plankton and of the larval fish diet. We cannot say how unusual were the circumstances we encountered, but we know that in terms of diatom numbers and larval fish diversity these conditions were not typical of March on the southern California continental shelf. That white croaker larvae appeared to find these conditions salubrious may be one reason this species is so successful in southern California (Love et al. 1984).

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[5]J. Beers, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. November 1986.

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NEW MARINE DECAPOD CRUSTACEANS FROM WATERS INFLUENCED BY HYDROTHERMAL DISCHARGE, BRINE, AND HYDROCARBON SEEPAGE

AUSTIN B. WILLIAMS[1]

ABSTRACT

Five species of decapod crustaceans new to science are described. These are caridean shrimps of the family Bresiliidae—*Alvinocaris markensis* from a Mid-Atlantic Rift Valley hydrothermal field, *A. muricola* from a cold brine seep at the foot of the West Florida Escarpment in the Gulf of Mexico, and *A. stactophila* from a hydrocarbon seep on the continental slope of the northern Gulf of Mexico, with a key to the species of *Alvinocaris*; a squat lobster of the family Galatheidae—*Munidopsis alvisca* from the Guaymas Basin and from the Juan de Fuca and Explorer ridges in the eastern Pacific; and a brachyuran crab of the family Bythograeidae—*Bythograea mesatlantica* from a Mid-Atlantic Rift Valley hydrothermal field. Species of both *Alvinocaris* and *Bythograea* are now known from the eastern Pacific and Mid-Atlantic. *Munidopsis* species are widely represented in the world oceans.

Deep ocean hydrothermally active fields and waters influenced by brine and hydrocarbon seeps continue to yield species new to science. Such environments were unknown until explored with the aid of submersible research vessels from which observations and collections could be accomplished. The species of decapod crustaceans reported here come from hydrothermal fields in the Mid-Atlantic Rift Valley, the Guaymas Basin in the Golfo de California, and Juan de Fuca and Explorer Ridges in the northeastern Pacific, a cold brine seep at the foot of the West Florida Escarpment, and a hydrocarbon seep on the continental slope of the northern Gulf of Mexico. These are scattered localities that exhibit diverse environmental conditions but that are bound together by the common thread of chemotrophic food chains (Childress et al. 1986; Brooks et al. 1987).

The material from the Mid-Atlantic Rift Valley, West Florida Escarpment, and Guaymas Basin was observed and collected by scientists working with the aid of the DSRV *Alvin* and RV *Atlantis II* based at the Woods Hole Oceanographic Institution. That from the northern Gulf of Mexico came from the Minerals Management Service Northern Gulf of Mexico Outer Continental Slope (MMS/NGOMCS) Regional Office Project, involving observation and collection of material by scientists from LGL Ecological Research Associates and Texas A&M University, with the aid of the submersible research vessel *Johnson-Sea-Link* and its support vessels. Specimens from Explorer and Juan de Fuca Ridges were collected with the aid of the Canadian DSRV *Pisces IV* and its support vessels.

All specimens studied are deposited in the Crustacean Collection of the United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

CARIDEA: BRESILIIDAE

Alvinocaris Williams and Chace, 1982

Three species of bresiliid shrimps described below as new to science are placed in the heretofore monotypic genus *Alvinocaris*. Certain features of these species necessitate minor changes in the generic diagnosis by Williams and Chace (1982) as follows: Rostrum with or without ventral teeth. Telson with 2–5 pairs of principal spines on posterior margin. Strong median sternal spine between posterior pair of pereopods.

Moreover, the branchial formula seems uniformly fixed in this genus as well as in the genus *Rimicaris* Williams and Rona, 1986. The arrangement, figured in Williams and Chace (1982) and Williams and Rona (1986) may be described as follows:

Phyllobranchs extensively developed in 2 series; asymmetrically Y-branched pleurobranchs with relatively short ventral and progressively longer and more expansive dorsal ramus associ-

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ated with pereopods 1–5; smaller and more nearly symmetrical U-branched arthrobranchs of more nearly uniform size associated with third maxilliped and pereopods 1–4.

Key to Known Species of *Alvinocaris*

1. Telson with terminal margin slightly concave in midline and bearing 3–5 pairs of principal spines .... *A. lusca* Williams and Chace

   Telson with terminal margin convex and bearing only 2 pairs of principal spines ... 2

2. Rostrum with ventral margin bearing 0–1 subterminal ventral spines .... *A. stactophila* new species

   Rostrum with ventral margin bearing 4 or more subterminal ventral spines 3

3. Abdominal segment 3 with pleural margin entire ..... *A. markensis* new species

   Abdominal segment 3 with pleural margin obscurely serrate .... *A. muricola* new species

Alvinocaris markensis new species

Figures 1, 2, 7

Material.—USNM 234286, Holotype ♀ (crushed), USNM 234287, Paratypes, 2 ♀ (damaged), Mid-Atlantic Rift Valley about 70 km south of Kane Fracture Zone (see Leg 106 Shipboard Scientific Party [1986]; Ocean Drilling Program Leg 106 Scientific Party [1986]), 23°22.09'N, 44°57.12'W, 3,437 m, *Alvin* Dive 1683, MARK vent, Stn. 1, scoop, 30 May 1986, pilot D. Foster, observers S. Humphris and J. Edmond. From NSF Ocean Drilling Program-Leg 106, NSF Grant OCE-8311201 to J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—Holotype ♀, postorbital carapace length 4.16, rostrum 2.3, maximum carapace height 3.3, total length about 15.6. Paratype ♀, same 2.7, 1.6, 2.4, 10.9.

Description.—Integument extremely thin, membranous, shining, with a few minute punctations. Rostrum (Fig. 1*a*, *b*) almost straight, slightly elevated above horizontal in distal half, sharply pointed tip usually reaching to between midlength of second and tip of third peduncular articles of antennule; dorsal margin raised into thin serrate crest containing 12–17 teeth, strongest in central sector of row, with about 1/3 length of crest continued onto carapace; ventral margin less prominent and armed with 5–8 subterminal teeth; tooth formulas examined, 17/8 (holotype), 17/5, 12/5 (apparently some subterminal dorsal teeth fused); strong lateral carina broadened proximally and confluent with orbital margin. Carapace with acute antennal spine distinct; pterygostomian spine acuminate and prominent. Indistinct antennal groove curving ventrad to intersect associated indistinct groove at about midlength of carapace and continuing posteriad.

Abdomen of female (Fig. 1*c*) apparently broadly arched dorsally (all specimens examined are crushed), gradually tapering posteriorly, narrowest part of sixth somite about 1/2 width of first somite; pleura of 3 anterior somites broadly rounded, that of fourth somite drawn posterolaterally to strong acuminate spine flanked dorsally by 0 or 1 much more slender and smaller spine; posterolateral corner of fifth pleuron strongly acuminate to nearly right angled and flanked dorsally by 0–2 spines of variable size analogous to condition on somite 4, spine number possibly age related; sixth somite with middorsal length about 1.9 that of fifth, broad based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth somite with small erect spine on sternite and fifth with analogous strong, posteriorly directed spine. Telson (Fig. 1*d*) elongate subrectangular, length about 3.5 anterior width, 5.8 posterior width, and about 1.75 length of sixth somite, not including posterior spines; armed with 6–8 dorsolateral spines of nearly uniform size, sometimes bilaterally unequal in number; posterior margin convex, armed with 2 principal spines at each corner and 10–12 feathered strong setae on margin between.

Eyes (Fig. 1*a*, *b*) with cornea imperfectly developed, unfaceted though diffusely pigmented, globular to ovate in outline and with prominent spine on anterodorsal edge.

Antennular peduncle (Fig. 1*a*, *b*) reaching end of antennal scale; basal article 1.3 length of second and about 3.0 length of third, stylocerite well

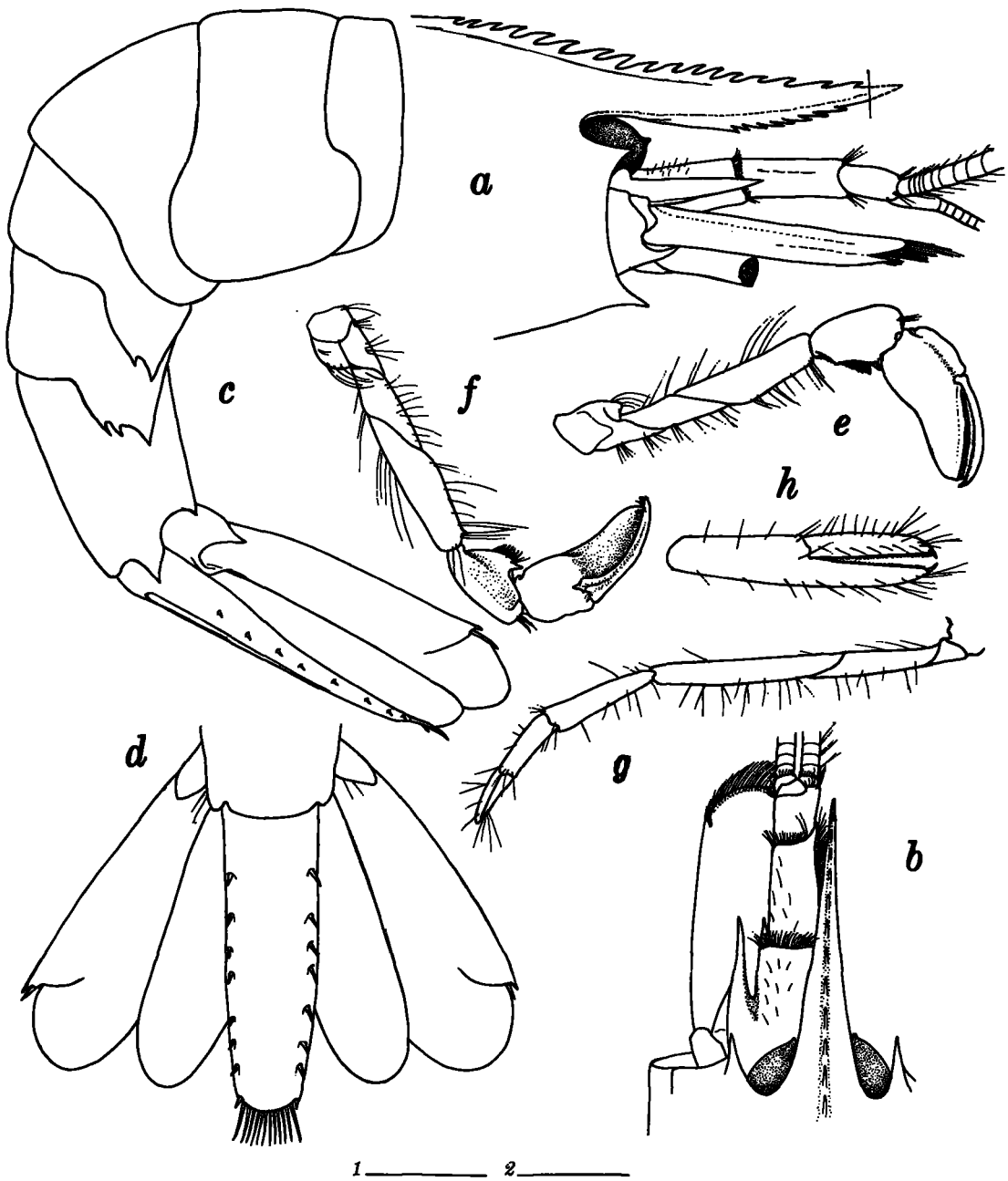

FIGURE 1.—*Alvinocaris markensis*, holotype ♀: *a* part of cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of left side; *c* abdomen, lateral; *d* tail fan; cheliped, *e* mesial, *f* lateral; *g* pereopod 2, *h* chela. Scales = 2 mm: 1 (*a*, *c*, *d*, *e*, *f*, *g*, *h*); 2 (*b*).

separated from peduncle, tapering to slender elongate tip reaching about 1/4 length of second article, basal article with distodorsal margin flanked by transverse row of setae, extended into strong lateral spine reaching level equal to that of stylocerite and closely appressed to second article; shorter second article with strong mesiodistal appressed spine. Dorsolateral flagellum about 1.5 length of carapace, thickened proximal half bearing conspicuous ventral setae; ventromesial flagellum somewhat more slender in lateral view and shorter.

Antennal scale (Fig. 1*a*, *b*) about 2.5 as long as wide, distolateral tooth falling short of distomesial apex of broadly rounded distal margin of blade; basal article with strong ventrolateral spine; flagellum slightly exceeding length of body (missing from holotype).

Mandibles (Fig. 2*g*) similar, with 2-segmented palp, incisor process broad and armed with 8 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 2*h*) with proximal endite asymmetrically oval-triangular, distal margin bearing many long setae; distal endite with narrowed base but broadened distally, armed with many (about 37) short spines on mesial margin and with scattered longer spinules marginally and submarginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and 1 shorter submarginal spine on distal branch.

Second maxilla (Fig. 2*i*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow somewhat twisted palp, scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, shorter setae along entire lateral margin; posterior lobe narrowly ovate-triangular, fringed on blunt tip and adjacent mesial margin by strikingly long, tangled, strong setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 2*j*, partly flattened view) with irregularly fusiform endite, short palp much exceeded in length and size by leaflike exopod, epipod obscurely bilobed.

Second maxilliped (Fig. 2*k*, *l*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, tip of exopod exceeding leaflike epipod.

Third maxilliped (Fig. 2*m*, *n*) slender, 5-segmented, reaching beyond antennular peduncle; terminal segment trigonal in cross section, tapered distally, bearing 3 terminal spines, oblique tracts of dense setae along mesial surface; similar tract of setae on carpus and another less conspicuous group on merus-ischium, latter with distolateral spine at articulation with carpus; exopod much reduced, ovate-triangular, without lash.

First pereopods (Fig. 1*e*, *f*) chelate, subequal; fingers curved ventrally and slightly laterad; dactyl much more slender than and slightly longer than fixed finger; mesial surface of each finger convex, lateral surface deeply concave; prehensile surfaces uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory hairs mesial to cutting edges, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around its external edge. Leg not reaching tip of third maxilliped and exceeding antennal peduncle. Palm of holotype female inflated, length slightly greater than height and shorter than fingers (0.60); low ridge ending in small hooked spine on proximomesial surface near articulation with carpus. Carpus longer than palm; bearing oblique ventral crest ending in strong distoventral spine and flanked mesially by patch of setae on triangular raised area; rectangular distal notch above spine followed by oblique distomesial margin leading to poorly defined spine at condyle articulating with palm; distolateral margin with rounded ventral corner leading to sinuous border above it bearing 2 lobes near articulation with palm. Merus somewhat swollen is distal half and bearing small distomesial spine, distinct from ischium but fused to it.

Second pereopod (Figs. 1*g*, *h*; 7*l*) shorter and more slender than first, but reaching beyond antennal peduncle by about length of fingers. Fingers slightly shorter than palm, similar in size and shape; opposed edges without gape, each spineless proximally, but distal half pectinate with single row of spines directed obliquely distad and increasing slightly in size to end in noticeably stronger spine crossing opposite member when closed. Carpus slender, about 0.9 length of chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 2*a–f*) similar in length and structure, third reaching distal edge of antennal scale. Length articles of these legs in holotype ♀, mm:

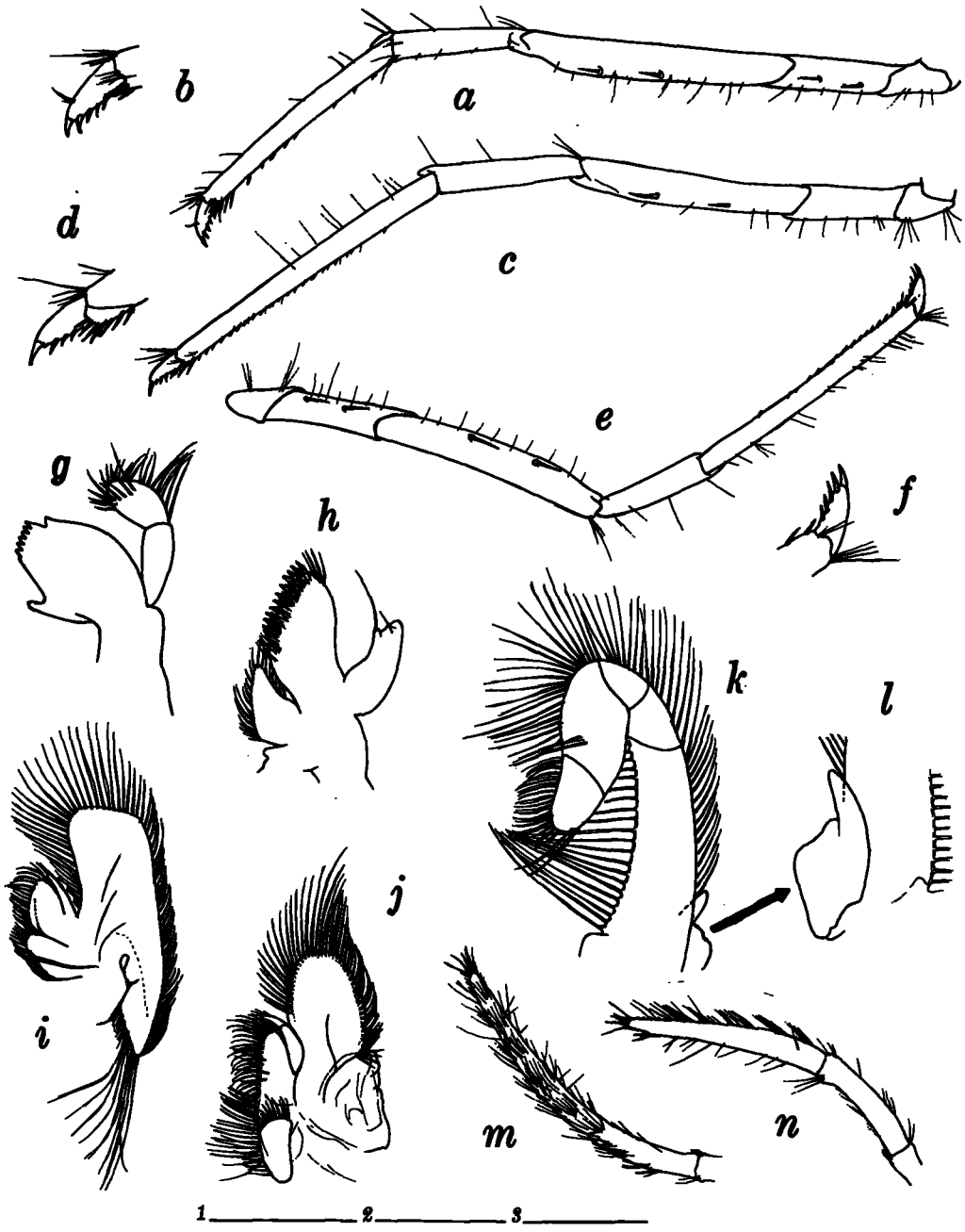

FIGURE 2.—*Alvinocaris markensis*, holotype ♀: *a* pereopod 3, *b* dactyl; *c* pereopod 4, *d* dactyl; *e* pereopod 5, *f* dactyl; *g* mandible; *h* maxilla 1; *i* maxilla 2; *j* maxilliped 1 partly flattened; maxilliped 2, *k* endopod, ventral, *l* part of exopod dorsal; maxilliped 3, *m* ventral, *n* dorsal, distal articles only. Scales: 1(*k*, *l*) = 1 mm; 2 (*b*, *d*, *f*, *g*, *h*) = 1 mm; 3 (*a*, *c*, *e*, *i*, *j*, *m*, *n*) = 2 mm.

	ischio-merus	*carpus*	*propodus*	*dactyl*
3rd	6.14	2.56	3.78	0.64
4th	5.76	2.18	4.12	0.70
5th	5.44	2.30	5.44	0.64

Each short dactyl armed with 5 spines on flexor surface, grading from small proximally to longest and strongest distally, often a sensory seta on extensor surface. Propodi with setae along flexor surface progressively more crowded distally. Carpi with distodorsal extension projecting as a stop along proximal part of propodal extensor surface. Third leg stronger, at least in merus-ischium, than fourth and fifth; merus of third and fourth with closely appressed ventral spine at 1/2 and 3/4 length, that of fifth with spines at 1/3 and 2/3 length, distal spine strongest in each case; ischium of third and fourth leg with 2 spines in line with those on merus.

Pleopods well developed, pair 1 with endopods about half length of exopods, tapering to acute tip; appendices internae simple, that of pair 5 with blunt tip.

Uropod (Fig. 1*d*) with rami subequal in length, slightly exceeding distal end of telson, lateral ramus with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Remarks.—Remarks are given in the account for *A. stactophila*.

Etymology.—The name is taken from an acronym for the site of collection in the Mid-Atlantic Ridge Valley about 70 km south of an area known as the Kane Fracture Zone, "MARK", and the Latin genitive suffix "ensis".

Alvinocaris muricola new species

Figures 3, 4, 7

Material.—USNM 234288, Holotype ♂ (cephalothorax and abdomen broken apart), USNM 234289, Allotype ♀, West Florida Escarpment, 26°01'N, 84°54.61'W, 3,277 m, *Alvin* Dive 1754, 15 October 1986, pilot W. Sellers, observers R. Carney and B. Hecker. USNM 234290, Paratype ♀, West Florida Escarpment, same locality, *Alvin* Dive 1753, 14 October 1986, pilot P. Tibbetts, observers R. Carney and G. Knauer. All from Barbara Hecker, Lamont Geological Observatory, Columbia University, Palisades, NY.

Measurements in mm.—Holotype ♂, postorbital carapace length 6.4, rostrum 4.4, maximum carapace height 4.5. Allotype ♀, same, 6.4, rostrum broken, 5.6.

Description.—Integument thin, shining, minutely punctate. Rostrum (Fig. 3*a*, *b*) almost straight to slightly upturned in distal half, sharply pointed tip reaching to proximal part of third peduncular article of antennule; dorsal margin raised into thin serrate crest containing 17-21 teeth varying from obliquely erect in proximal part to nearly horizontal, shorter and more distant distally, about 1/3 length of crest continued onto carapace; ventral margin much less prominent and armed with row of 6 correspondingly smaller subterminal teeth, sometimes obscure; lateral carina broadened proximally and confluent with orbital margin. Carapace (Fig. 3*a*) with broad based but slender, acuminate antennal spine; pterygostomian spine correspondingly acuminate and prominent. Prominent anterior antennal carina curving posteroventrally to intersect obliquely with carina extending from pterygostomian spine at about midlength of carapace, associated groove continuing indistinctly posteriad.

Abdomen (Fig. 3*d*, *e*, *f*) of both male and female broadly arched dorsally, gradually tapering distally, narrowest part of sixth somite less than 2/3 (0.60) width of first somite; pleura of 3 anterior somites broadly rounded, margin of third slightly serrated, that of fourth somite drawn posterolaterally to strong spine flanked dorsally by 0–3 more slender and smaller spines and preceded on ventral margin by 0–2 small spines; number, position, and shape of either lateral or ventral spines may be asymmetrical; posterolateral corner of fifth pleura acuminate and flanked dorsally by 1 or 2 spines analogous to those on somite 4; sixth somite with middorsal length about 1.7 that of fifth, broad-based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth and fifth somites each with strong, posteriorly directed spine on sternite. Telson (Fig. 3*g*) elongate subrectangular, length about 3.0 anterior width, 6.8 posterior width, and about 1.4 length of sixth somite, not including posterior spines; armed with 7 dorsolateral spines of nearly uniform size; posterior margin convex, armed with 2 principal spines at each corner and 10 or 11 feathered strong setae on distal margin between.

Eyes (Fig. 3*a*, *b*) with cornea imperfectly developed, unfaceted though diffusely pigmented,

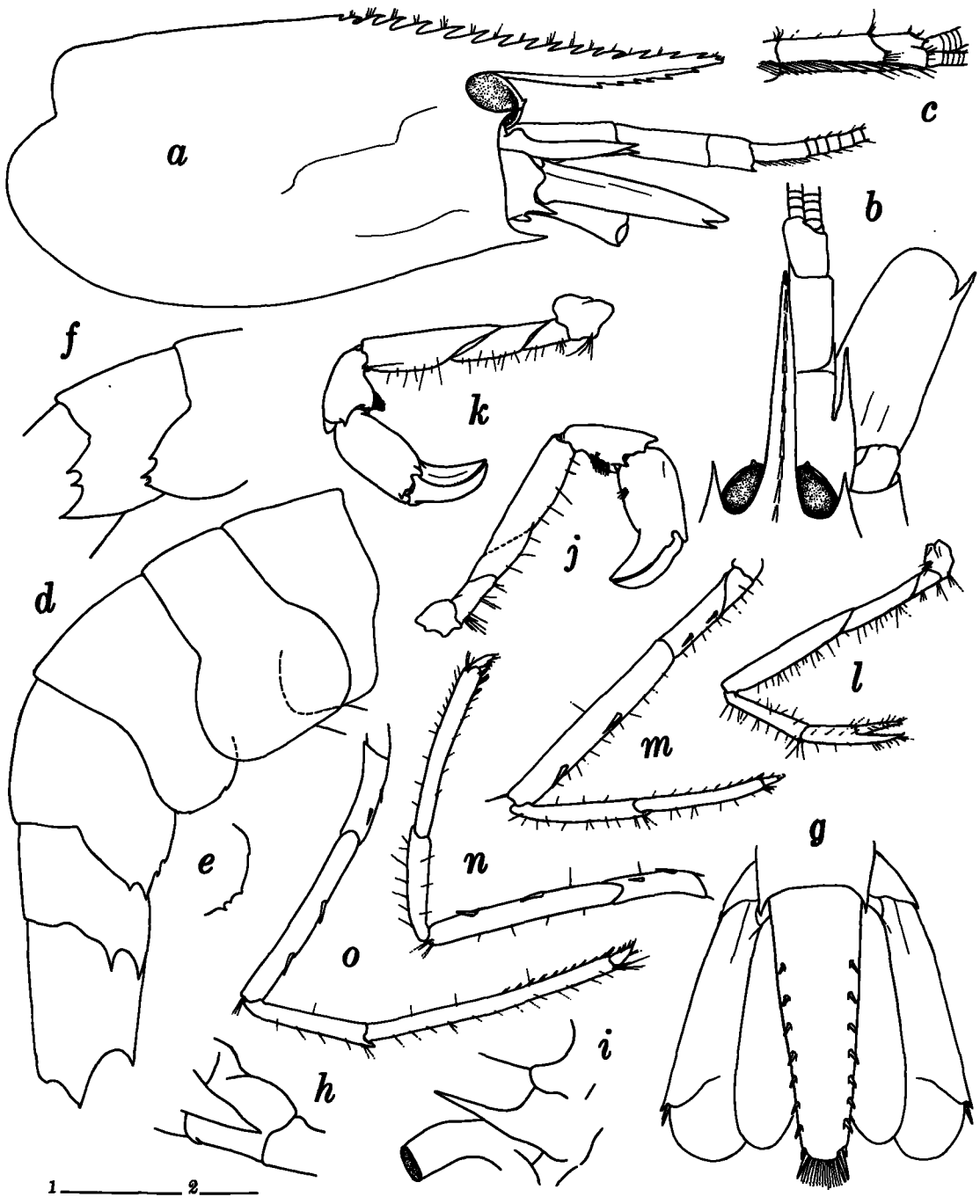

FIGURE 3.—*Alvinocaris muricola*, holotype ♂: *a* cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of right side; *c* antennular peduncle, distal articles, mesial; abdomen with variations in spination of pleural margins (of allotype ♀), *d* lateral, *e* margin of pleuron 3 from opposite side, *f* (of holotype ♂) segments 4 and 5; *g* tail fan; *h* median sternal spine between fifth pereopods; *i* median sternal spine on abdominal segment 5; cheliped, *j* mesial, *k* lateral; *l*, *m*, *n*, *o* pereopods 2, 3, 4, 5. Scales = 1 mm: 1 (*a–g*, *j–o*); 2 (*h*, *i*).

ovate in outline, though fused to each other mesially, and each with a short upturned spine on anterior surface.

Antennular peduncle (Fig. 3*a*, *b*, *c*) reaching beyond end of antennal scale; basal article 1.1 as long as second and about 2.5 as long as third, all measured on ventral margin; stylocerite well separated from peduncle, tapering to slender elongate tip reaching tip of distolateral spine on basal article; latter exceeding distodorsal margin of article, fringed by transverse subdistal row of setae, and closely appressed to second article, distomesial spine much smaller; shorter second article with stronger mesiodistal spine. Dorsolateral flagellum about length of carapace, thickened in basal 2/3, with annulations, except at base, longer in female than in male and much longer than in whiplike distal part; ventromesial flagellum somewhat shorter and with annulations of variable but shorter length.

Antennal scale (Fig. 3*a*, *b*) about twice as long as wide, distolateral tooth strong, falling slightly short of broadly rounded distal margin of blade; basal article with acute distal spine ventrally; flagellum (broken in material studied) probably slightly exceeding length of body.

Mandibles (Fig. 4*a*) similar, with 2-segmented palp, incisor process broad and armed with 8 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 4*b*) with proximal endite asymmetrically oval-triangular, distal margin bearing many long setae; distal endite with narrowed base but broadened distally, armed with many (about 30) short spines on mesial margin and with scattered longer spinules submarginally and marginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and 1 shorter submarginal spine on distal branch.

Second maxilla (Fig. 4*c*, *d*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow, somewhat twisted palp; scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, uniformly shorter setae along entire lateral margin; posterior lobe narrow and acuminate, fringed on blunt tip and adjacent mesial margin by strikingly long, strong, tangled setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 4*e*, *f*) with irregularly fusiform endite, short palp concealed and much exceeded in length and size by leaflike exopod, epipod obscurely bilobed; indistinct mesial lobule on exopod possibly representing incipient lash.

Second maxilliped (Fig. 4*g*, *h*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, exopod barely exceeding leaflike epipod.

Third maxilliped (Fig. 4*i*, *j*) slender, 5-segmented, reaching beyond antennular peduncle; terminal article trigonal in cross section, tapered distally, bearing 3 spines, transverse tracts of dense setae along mesial surface; similar tract of setae on carpus and another conspicuous group mesiodistally on merus-ischium, latter with stout distolateral spine at articulation with carpus; exopod much reduced, subtriangular, without lash.

First pereopods (Figs. 3*j*, *k*; 7*f*–*k*) chelate, subequal and sexually dimorphic, at least in fully mature individuals; fingers curved ventrally and slightly laterad; dactyl more slender than and with level of tip slightly shorter than or equal to that of fixed finger; mesial surface of each finger convex, lateral surface concave, with opposed surfaces uniformly offset; closing without gape, each armed on prehensile edge with row of almost uniform teeth so closely set as to be almost contiguous, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around its external edge; line of sensory hairs mesial to cutting edges. Leg shorter than to almost equaling third maxilliped. Palm of holotype male inflated laterally, but apparently somewhat irregularly concave mesially, length 1.4 greatest height and longer than fingers; palm relatively shorter in allotype female, 0.3 length of fingers. Carpus shorter than palm, with oblique ventral crest ending in strong distolateral spine, flanked mesially by patch of setae on polygonal raised area. Merus somewhat swollen in distal half, distinct from ischium but fused to it, neither armed.

Second pereopod (Figs. 3*l*; 7*e*) shorter and more slender than first, reaching about to end of antennal peduncle; fingers slightly longer than palm, similar in size and shape, opposed edges without gape, each pectinate with single row of teeth in distal half directed obliquely distad and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.16 longer than chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 3*m*, *n*, *o*) similar in length and structure, third reaching to tip of or

FIGURE 4.—*Alvinocaris muricola*, holotype ♂: *a* mandible; *b* maxilla 1; maxilla 2, *c* ventral, *d* palp dorsal; maxilliped 1, *e* ventral, *f* dorsal; maxilliped 2, *g* ventral, *h* dorsal; maxilliped 3, *i* ventral, *j* dorsal; *k* endopod of pleopod 1; *l* appendix masculina, pleopod 2. Scales: 1 (*e*, *f*, *g*, *j*, *o*, *k*, *l*) = 1 mm; 2 (*c*, *d*) = 1 mm; 3 (*l*) = 0.2 mm; 4 (*a*, *b*) = 0.2 mm.

slightly beyond antennal scale. Length articles of these legs in holotype ♂, mm:

	ischium	*merus*	*carpus*	*propodus*	*dactyl*
3rd	1.76	3.84	2.33	2.34	0.35
4th	1.60	3.52	1.98	3.04	0.06
5th	1.60	3.20	2.43	4.96	0.42

Each short dactyl armed with about 4–6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; carpus of each with distodorsal extension projecting as a stop along proximal part of propodal extensor surface; third leg stronger, at least in merus-ischium, than fourth and fifth, but propodus successively longer from third to fifth; merus of each with ventral spine at 1/3 and 2/3 length; ischium of third, fourth, and fifth leg with 2 spines in line with those on merus.

Pleopods well developed; first pair with endopods about 1/2 length of exopods in both sexes, narrowed into distomesial projection in male (Fig. 4*k*) but evenly tapered in female; appendix masculina (Fig. 4*l*) of second pair in male (holotype) armed with 7 slender spines extending beyond level of simple slender appendix interna; endopods of third to fifth in male and second to fifth in female with simple slender appendix interna, but that of fifth blunt tipped.

Uropod (Fig. 3*g*) with rami subequal in length, lateral ramus slightly exceeding distal end of telson, and with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Remarks.—Remarks are given in the account for *A. stactophila*.

Etymology.—The name is from the Latin "muria", brine, and "cola", inhabiting, for association of the species with cold brine seeping from the base of the West Florida Escarpment.

Alvinocaris stactophila new species

Figures 5, 6, 7

Material.—USNM 234291, Holotype ♂, USNM 234292, Allotype ♀, USNM 234293, Paratypes, 5 ♂, 2 ♀; north central Gulf of Mexico about 129 km (80 miles) S of Louisiana, 27°46.94'N, 91°30.34'W, 534 m, *Johnson-Sea-Link* Dive 1879, 28 September 1986, Bush Hill hydrocarbon seep. From Linda H. Pequegnat and Randall Howard, LGL Ecological Research Associates, Bryan, TX, supported by partial funding for Minerals Management Service-Northern Gulf of Mexico contract 14-12-0001-30212.

Measurements in mm.—Holotype ♂, postorbital carapace length 7.0, rostrum 2.7, maximum carapace height 5.3, total length about 25. Allotype ♀, same 6.8, 2.0, 5.9, 24. Paratype ♂, same 4.2, 1.9, 3.2, total length not measured; paratype ♀, same, 4.9, 2.0, 4.1.

Description.—Integument thin, shining, minutely punctate. Rostrum (Fig. 5*a*, *b*) almost straight, imperceptibly elevated above horizontal in distal half, sharply pointed tip usually reaching proximal level of second peduncular article of antennule, but sometimes to proximal part of third peduncular article; dorsal margin raised into thin serrate crest containing 12–17 teeth, strongest in central sector of row, with about 1/2 length of crest continued onto carapace; ventral margin less prominent and armed with 0 or 1 subterminal tooth; sample tooth formulas 11/1, 12/0, 14/1, 17/1; lateral carina broadened proximally and confluent with orbital margin. Carapace (Fig. 5*a*, *b*) with buttressed acuminate antennal spine distinct; pterygostomian spine acuminate and prominent. Prominent anterior antennal carina curving posteroventrally to intersect obliquely with carina extending from pterygostomial spine at about midlength of carapace, associated groove continuing indistinctly posteriad.

Abdomen (Fig. 5*d*) of both male and female broadly arched dorsally, gradually tapering distally, narrowest part of sixth somite less than 1/2 (0.44) width of first somite; pleura of 3 anterior somites broadly rounded, that of fourth somite drawn posterolaterally to acuminate spine flanked dorsally by 0–3 much more slender and smaller spines; posterolateral corner of fifth pleuron varying from strongly acuminate to nearly rectangular and flanked dorsally by 2–5 spines analogous to those on somite 4; sixth somite with middorsal length about 1.8 that of fifth, broad-based midlateral spine overlapping base of telson, smaller posterolateral spine acute; fourth and fifth somites each with strong, posteriorly directed spine on sternite. Telson (Fig. 5*e*) elongate subrectangular, length about 2.8 anterior width, 5.2 posterior width, and about 1.7 length of sixth somite, not including posterior spines; armed with 5–8 dorsolateral spines of

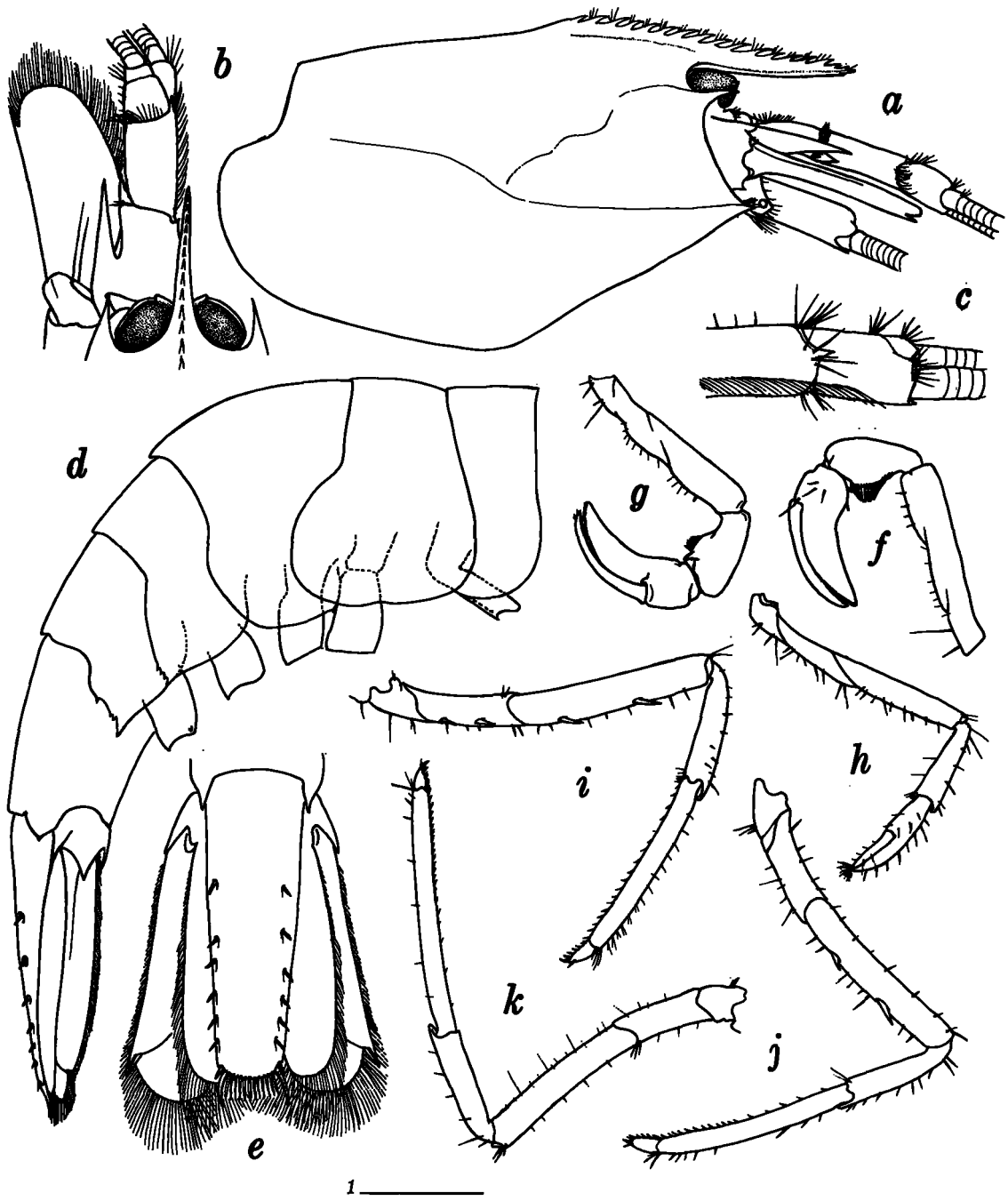

FIGURE 5—*Alvinocaris stactophila*, holotype ♂: *a* cephalothorax and anterior appendages, lateral; *b* rostrum, eye, antennular peduncle, antennal scale, dorsal of left side; *c* antennular peduncle, distal articles, mesial; *d* abdomen, lateral; *e* tail fan. Allotype ♀: cheliped, *f* mesial, *g* lateral; *h*, *i*, *j*, *k* pereopods 2, 3, 4, 5. Scale = 2 mm.

nearly uniform size, occasionally unequal in number on either side; posterior margin convex, armed with 2 principal spines at each corner and 8–12 feathered strong setae on distal margin between.

Eyes (Fig. 5*a*, *b*) with cornea imperfectly developed; unfaceted though diffusely pigmented in adults, but with internal facetlike pattern in smaller individuals; ovate in outline though fused to each other mesially, and each with an upturned spine on anterodorsal surface.

Antennular peduncle (Fig. 5*a*, *b*, *c*) reaching beyond end of antennal scale; basal article 1.3 length of second and about 2.2 length of third, all measured on dorsal margin; stylocerite well separated from peduncle, tapering to slender elongate tip variably reaching as far as midlength of second article; basal article with distodorsal margin exceeded by rostral tip though extended into strong lateral spine reaching level equal to that of stylocerite and closely appressed to second article, much smaller distomesial spine slightly divergent; shorter second article with stronger mesiodistal spine. Dorsolateral flagellum about twice length of carapace, thickened in basal half; ventromesial flagellum somewhat shorter.

Antennal scale (Fig. 5*a*, *b*) about twice as long as wide, distolateral tooth strong, falling short of broadly rounded distal margin of blade; basal article with small distal spine ventrally; flagellum slightly exceeding length of body.

Mandibles (Fig. 6*a*) similar, with 2-segmented palp, incisor process broad and armed with 7 marginal teeth, slender molar process simple, divergent, its narrowly rounded tip minutely setose.

First maxilla (Fig. 6*b*) with proximal endite asymmetrically oval-triangular, distal margin bearing about 25 long setae; distal endite with narrowed base but broadened distally, armed with many short spines on mesial margin and with scattered longer spinules submarginally and marginally beyond either end of spine row; palp scarcely bifurcated, with long distal spine on obsolescent proximomesial branch and shorter adjacent submarginal spine and tangled setae on distal branch.

Second maxilla (Fig. 6*c*) with proximal endite represented by 2 similar lobes; distal endite subtriangular, expanded mesiodistally and paralleled laterally by narrow somewhat twisted palp; scaphognathite with anterior lobe rectangulo-ovate, fringed with uniformly long, silky setae on anterior and mesial borders, uniformly shorter setae along entire lateral margin, posterior lobe narrow and acuminate, fringed on blunt tip and adjacent mesial margin by strikingly long, tangled strong setae preceded proximally by shorter setae similar to those on lateral margin.

First maxilliped (Fig. 6*d*, *e*) with irregularly fusiform endite, short palp concealed and much exceeded in length and size by leaflike exopod, epipod obscurely bilobed; indistinct mesial lobule on exopod possibly representing incipient lash.

Second maxilliped (Fig. 6*f*, *g*) somewhat pediform but flattened, mesial margin of articles bearing long, feathered setae, mesial surface of terminal article densely setose, exopod barely exceeding leaflike epipod.

Third maxilliped (Fig. 6*h*, *i*, *j*) slender, 5-segmented, reaching beyond antennular peduncle; terminal article trigonal in cross section, tapered distally, bearing 3 spines, transverse tracts of dense setae along mesial surface; similar tract of setae on carpus and another less conspicuous group on merus-ischium, latter with stout distolateral spine at articulation with carpus; exopod much reduced, subtriangular, without lash.

First pereopods (Figs. 5*f*, *g*; 7*c*, *d*) chelate, subequal and sexually dimorphic, at least in fully mature individuals; fingers curved ventrally and slightly laterad; dactyl more slender than fixed finger, tips varying slightly in relative length; mesial surface of each finger convex, lateral surface concave; prehensile surfaces uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory hairs mesial to cutting edges, acute tip of dactyl slightly spooned by elongate teeth slanted distad and curving around external edge. Leg exceeding third maxilliped by length of fingers in holotype male, but shorter than third maxilliped in other individuals. Palm inflated in holotype male, length 1.4 greatest height and longer than fingers; palm relatively shorter in allotype female and other individuals examined, 0.3 length of fingers. Carpus shorter than palm in holotype but longer than palm in remainder of specimens examined, bearing oblique ventral crest ending in strong distolateral spine and flanked mesially by patch of setae on polygonal raised area; notch above spine smoothly concave and opposing low ridge ending in small rounded spine on heel of palm; shallowly concave anteromesial margin of carpus leading dorsally to 2 low rounded lobes. Merus somewhat swollen in distal half, distinct from ischium but fused to it, neither armed.

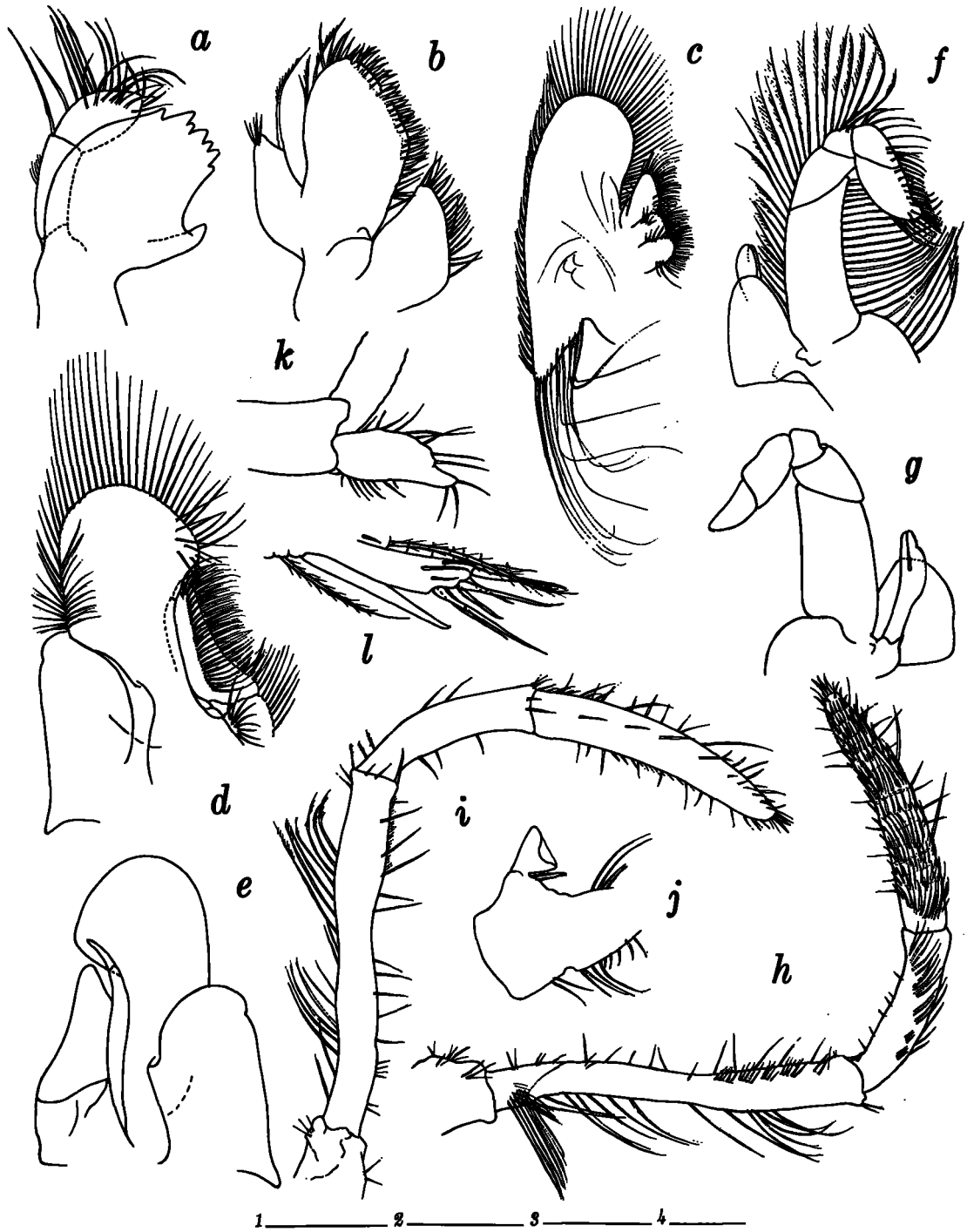

FIGURE 6.—*Alvinocaris stactophila*, allotype ♀: *a* mandible; *b* maxilla 1; *c* maxilla 2; maxilliped 1, *d* ventral, *e* dorsal; maxilliped 2, *f* ventral, *g* dorsal; maxilliped 3, *h* ventral, *i* dorsal, *j* exopod. Paratype ♂: *k* endopod of pleopod 1; *l* appendix masculina, pleopod 2. Scales: 1 (*d–g*, *k*) = 1 mm; 2 (*a*, *b*) = 0.5 mm; 3 (*l*) = 0.3 mm; 4 (*c*) = 1 mm.

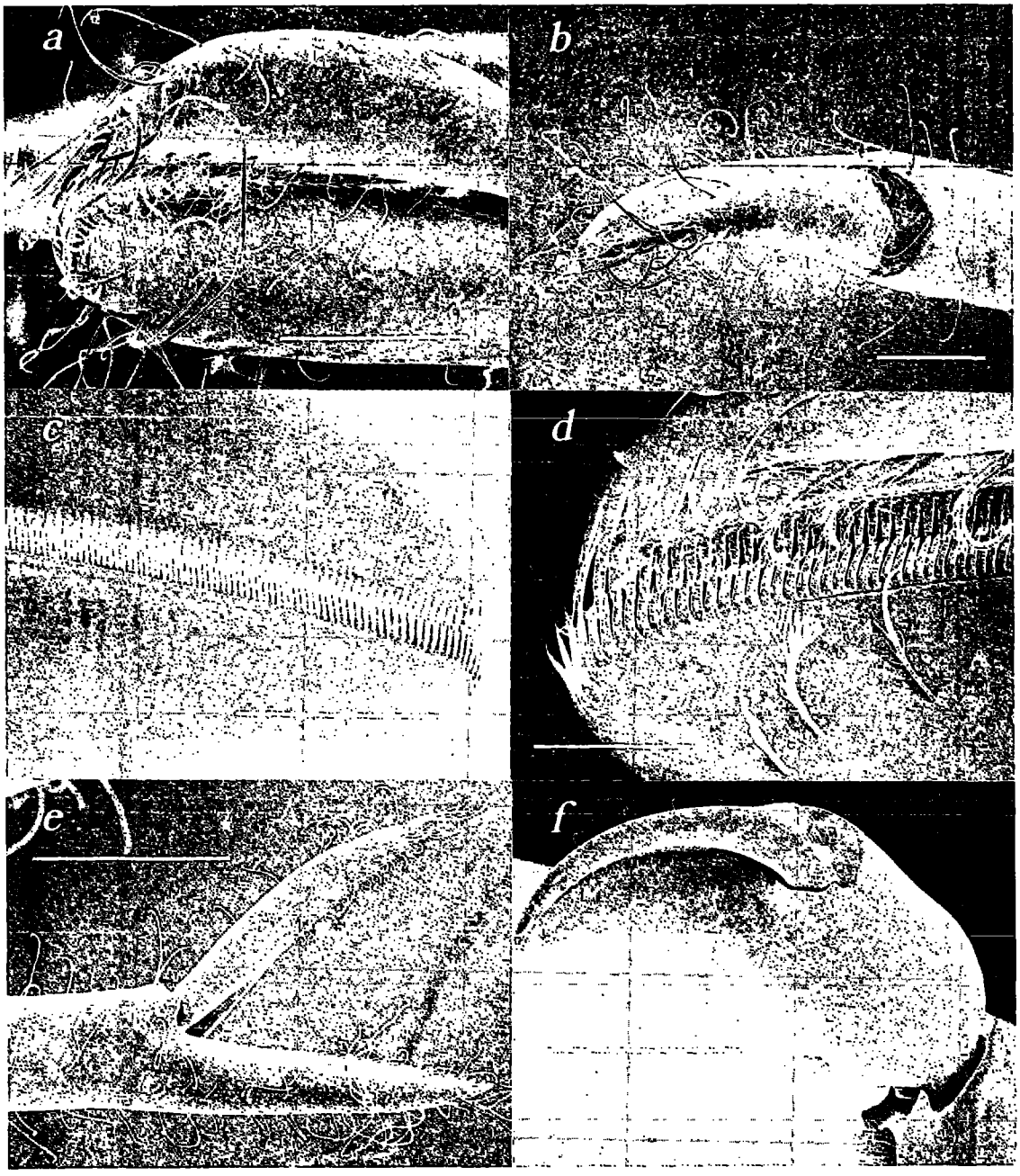

FIGURE 7.—Parts of *Alvinocaris* chelae viewed by SEM. *A. stactophila*: fingers of small chela, *a* mesial, *b* dorsal; fingers of large chela showing finely toothed opposed edges near tips, *c* mesial, teeth flush with convex surface, *d* lateral, teeth marginal on spooned tips, with points rounded on dactyl, acute on fixed finger. *A. muricola*: *e* fingers of small chela, lateral; *f* large chela and distal part of carpus, lateral. Scales: 100 μm, *d*; 200 μm, *a–c*; 500 μm, *e*; 1 mm, *f*.

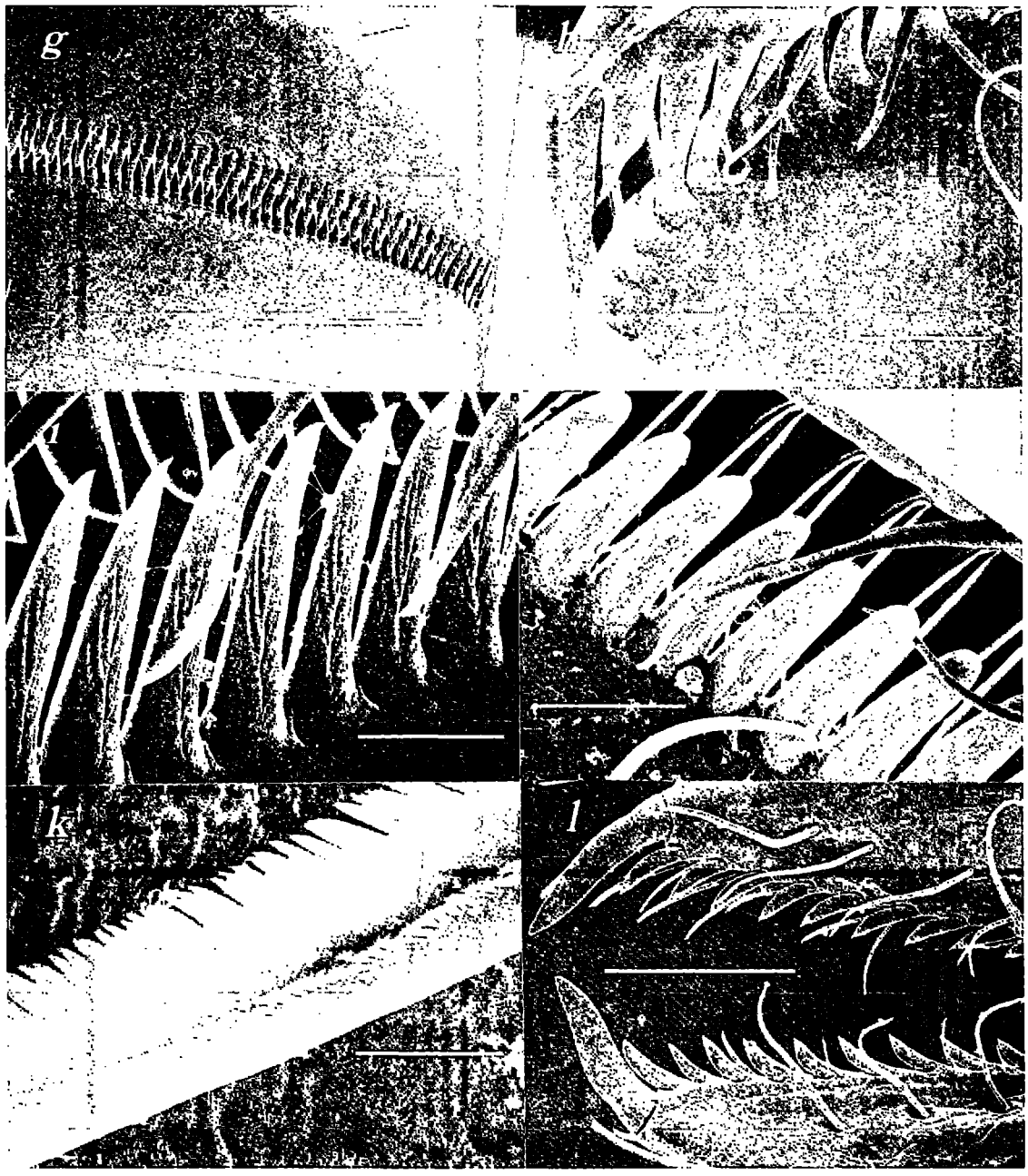

FIGURE 7.—*Continued.—Alvinocaris muricola*: fingers of large chela showing finely toothed opposed edges near tips, *g* teeth flush with convex mesial surface, *h* spooned lateral surface of same, points rounded on dactyl, acute on fixed finger; close-up lateral view of teeth and associated sensory setae, teeth of fixed finger in foreground and of dactyl in background, *i* near distal end of fingers, *j* near midlength of fingers; *k* sensory seta showing 2 rows of sensillae on concave surface. *A. markensis*: *l* fingers of small chela, mesial view of distal part. Scales: 3 μm, *k*; 20 μm, *i*; 30 μm, *j*; 50 μm, *h*; 100 μm, *l*; 200 μm, *g*.

Second pereopod (Figs. 5*h*; 7*a*, *b*) shorter and more slender than first, reaching to between midlength and end of antennal peduncle; fingers slightly longer than palm, similar in size and shape, opposed edges without gape, each pectinate with single row of teeth in distal half directed obliquely distad and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.2 longer than chela; merus and ischium unarmed.

Third to fifth pereopods (Fig. 5*i*,*j*, *k*) similar in length and structure, third reaching beyond antennal scale by about 0.3 length of propodus. Length articles of these legs in allotype ♀, mm:

	ischio-merus	*carpus*	*propodus*	*dactyl*
3rd	4.48	2.30	3.20	0.48
4th	4.89	2.18	3.39	0.48
5th	4.16	2.24	4.22	0.48

Each short dactyl armed with about 6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; carpus of each with distodorsal extension projecting as a stop along proximal part of propodal extensor surface; third leg stronger, at least in merus-ischium, than fourth and fifth; merus of third and fourth with ventral spine at 1/3 and 2/3 length, distal one strongest, fifth without spines; ischium of third with 2 spines in line with those on merus, that of fourth and fifth spineless.

Pleopods well developed, pair 1 with endopods about half length of expods in both sexes, endopod of male (Fig. 6*j*) with asymmetrical mesial extension, that of female tapering to acute tip; pair 2 with appendix masculina of male (Fig. 6*k*) bearing distal cluster of about 9 strong straight spinules extending beyond level of simple slender appendix interna.

Uropod (Fig. 5*e*) with rami subequal in length, slightly exceeding distal end of telson, lateral ramus with movable spine mesial to smaller distolateral tooth, diaeresis sinuous.

Etymology.—The name is from the Greek "stactos", oozing out or trickling, and "philos", to love, for association of the species with hydrocarbons seeping from the substrate.

Remarks.—*Alvinocaris lusca* and the three new species of *Alvinocaris* described here exhibit minor differences that are highlighted in the key to species given above, but their similarities seem far more significant; i.e., general body appearance and strength of integument, shape of rostrum (although that of *A. stactophila* sometimes lacks ventral teeth), shape and general armature of tail fan, blindness, and general structure of appendages, including mouthparts. Some minor differences that may be mentioned are features such as number of incisor teeth on the mandible, number of spines on the first maxilla, shape of the second maxilla, lack of meral spines on pereopod 5 in *A. stactophila*, unequal distribution of spines on ischia of pereopods 3–5 in the three species, and shape of the endopod of male pleopod 1 and appendix masculina (though males of *A. markensis* are not yet known).

Each of these species lives in a distinctive benthic environment, but all share similarities that suggest dependence on a chemotrophic bacteria-based food chain (Childress et al. 1986). Van Dover et al. (in press) provide evidence from morphology, behavioral and gut content analyses of the similar *Rimicaris exoculata* Williams and Rona that indicates a bacterial diet grazed from surfaces of hydrothermal chimneys, although direct observations of bacteria within the digestive tract could not confirm this. The distinctively spoon-shaped chelae of the first pereopods of both *Alvinocaris* and *Rimicaris* species, with unbroken comb of exceedingly fine teeth on the prehensile edges, could be an adaptation for scooping or sweeping bacteria toward the mouthparts. Williams and Chace (1982) described the first chelae of *A. lusca* as convex on the extensor surface and concave on the flexor surface, but they also said (p. 142) that the outer surface of the fingers is convex and the inner surface concave. The latter is misleading because in full extension the convex side of the chela is mesial and the concave side lateral. It is not yet known how these appendages are used, but certainly the chelae can be folded compactly against the leg's proximal articles, and in the related *Rimicaris exoculata* and *R. chacei* (Williams and Rona 1986) these legs seem very mobile. Sensillae flanking prehensile surfaces of the fingers seem well adapted to aid feeding on finely particulate matter. Moreover, the species of *Rimicaris* have exceedingly setose mouthparts.

In species of both genera, the second pair of pereopods have much smaller chelae with fingers bearing long sensory setae and spines on the prehensile edges that are seemingly adapted for

grasping. For mobile animals of this morphological makeup, the most likely feeding methods in the stated environments would seem to be bacterial concentration, along with secondary predation and scavenging.

ANOMURA: GALATHEIDAE

Munidopsis alvisca new species

Figure 8

Material.—USNM 234294, ♀ Holotype, USNM 234301, ♀ Paratype, Guaymas Basin, Golfo de California, 27°00'N, 111°25'W, 2,008 m, *Alvin* Dive 1616, 8 August 1985, pilots J. Hardiman and R. Wilkes, observer J. F. Grassle. From J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

USNM 234295, ♂ Paratype, Explorer Ridge, Magic Mountain, 49°45.6'N, 130°16.16'W, 1,818 m, *Pisces IV* Dive P-1494, Coll. No. 1877, Gulati Gusher-base, 1 July 1984, pilots-observers, Witcombe, Johnson, Tunnicliffe. USNM 234296, ♀ ovig. Paratype, Explorer Ridge, Upper Magic Mountain, 49°45.5'N, 130°16.1'W, 1,812 m, *Pisces IV* Dive P-1497, Coll. No. 1873, Lunch Hour Vent, 4 July 1984, pilots-observers, Shepherd, Juniper, Johnson. USNM 234297, ♀ ovig. Paratype, same, Coll. No. 1875, Crab Vent. USNM 234298, ♀ ovig. Paratype, same, Coll. No. 1875. USNM 234299, 2 ♀ ovig. Paratypes, Juan de Fuca Ridge, Limbo Vent (= 3 m from Holland's Hillock Axial Seamount), 45°55'N, 130°03'W, 1,545 m, *Pisces IV* Dive P-1732, Coll. No. 1934, 2 August 1986, pilots-observers, K. Shepherd, R. Embley, J. Franklin. From Verena Tunnicliffe, Biology Department, University of Victoria, B.C., Canada.

Measurements in mm.—Holotype ♀, carapace length including rostrum 23.7, margin of orbit to posterior edge of carapace 18.6, maximum carapace width 15.7; Paratype ♀ 234301, same, 27.9, 20.8, 17.3; Paratype ♂ 234295, same, 13.8, 10.2, 8.4.

Description.—Carapace (Fig. 8*a*, *c*) exclusive of rostrum distinctly longer than broad, moderately arched transversely; anterior and posterior cervical grooves apparent, depression in anterior part of cardiac region; short moderately developed rugosities on each anterior branchial region, but more distinct and transversely developed rugae on each posterior branchial region, with tendency to being continuous across anterior and central part of cardiac region; posterior margin with median concavity. Rostrum narrowly triangular, concave dorsal surface smoothly curving to upturned tip exceeding eyestalks by more than twice their length, distinct carina bearing almost imperceptible scalelike rugae diminishing to obsolescence on gastric region. Frontal margin with broad angle lateral to eyestalk followed by concave raised and sparsely ornamented margin ending in antennal spine followed in turn by almost rectangular but acute anterolateral angle. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle, its rather angular tip minutely but bluntly bispinose.

Abdomen (Fig. 8*b*) unarmed; transverse ridge of segments 2 and 3 smooth, that of segment 4 obsolescent; segments 5 and 6 smooth.

Eyes (Fig. 8*a*, *c*) moderate in size; well exposed, smoothly ovate cornea cupped within broad based movable ocular peduncle extended into elongate mesiodorsal spine, directed obliquely upward at low angle and ornamented with tiny irregular obsolescent spinules, and much shorter mesioventral spine.

Basal article of antennular peduncle with distal margin irregularly crenulate, slender dorsolateral spine and broader lateral spine flanked by cluster of irregular small spinules, an obsolescent mesiodorsal spine present. Antennal peduncle with fixed basal article extended into stout, flat ventral spine and shorter crenulate lateral spine; succeeding articles short, second bearing stout lateral angle, third unarmed, fourth with scalloped distal margin, its dorsomesial projection spinelike.

Third maxilliped (Fig. 8*e*) with ischium shorter than merus, bearing mesial crest armed with finely uniform, evenly spaced corneous teeth. Basis with 2 low spines in line with crest on ischium. Merus with obsolescent spine at posteromesial corner, mesial margin usually with another at level of propodo-carpal joint, followed after an interval by an obscure tubercle, and then by a more prominent spine at base of convex distal margin; stronger spine at anterolateral corner; lateral margin broadly arched. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those two articles together, dense setation on dorsal surface of each, and distally on prehensile surface of propodus and dactyl. Sternite (Fig. 8*d*) at base of third maxil-

liped with convex crenulate anterior margin on mesial lobe, lateral lobe angular.

Epipods absent from pereopods.

Chelipeds (Fig. 8*f*) subequal, ornamented with variably ciliate rugosities tending to arrangement in longitudinal tracts; ischium with mesial ridge bearing subterminal spine and obsolescent irregular subsidiary spines; merus rough, bearing 3 mesial spines, 1 distodorsal spine, and a smaller distoventral spine; carpus with 2 spines in dorsolateral row paralleled by less prominent ventrolateral row; palm with spines on prominent

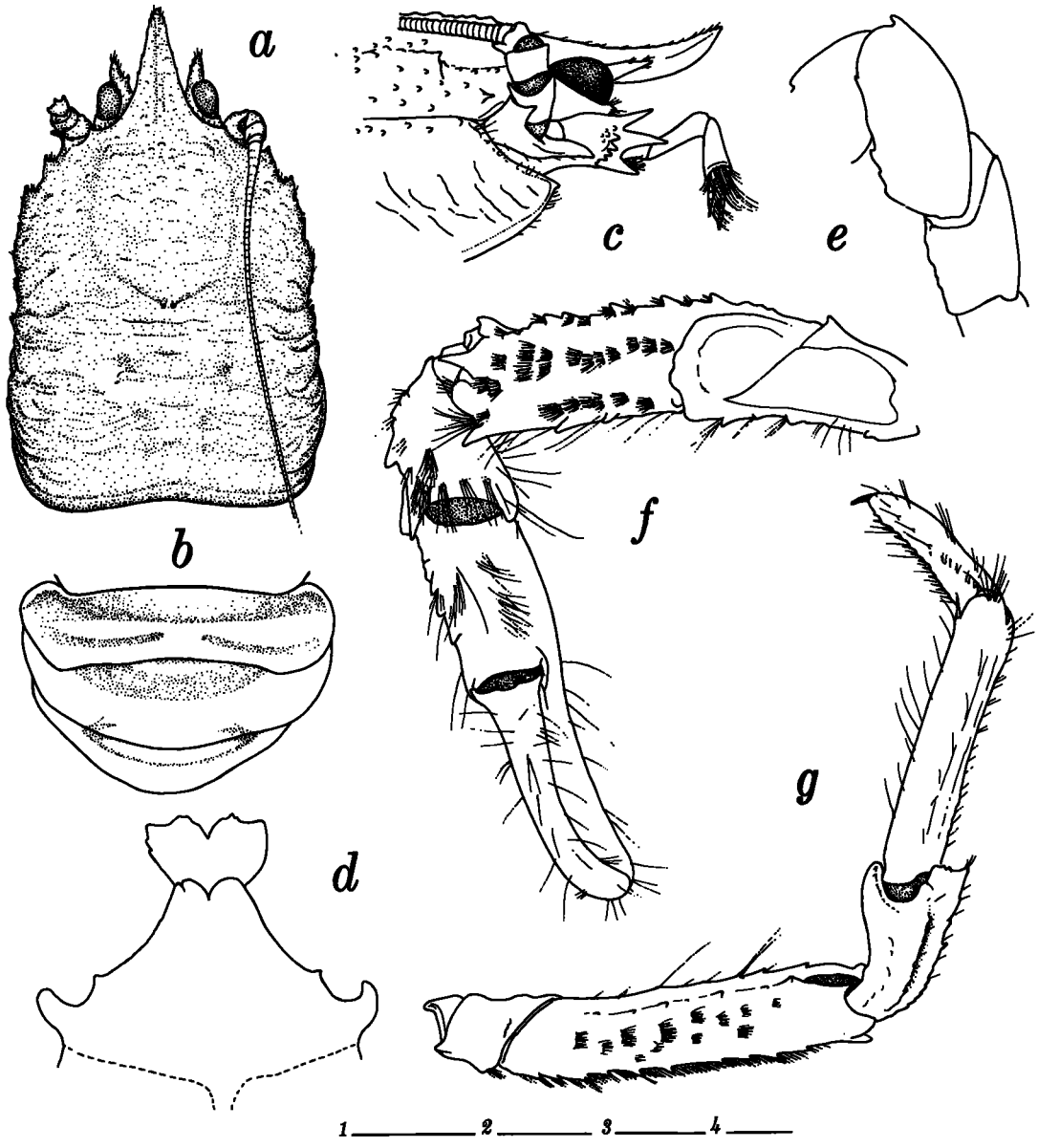

FIGURE 8.—*Munidopsis alvisca*, holotype ♀: *a* carapace, eyes and right antenna, dorsal; *b* abdomen, somites 2–4 in folded position; *c* part of cephalothorax and anterior appendages, lateral; *d* sternites at base of third maxilliped and chelipeds; *e* left third maxilliped, merus and ischium; *g* left second pereopod. Paratype ♀ 234301: *f* right cheliped. Scales: 1 (*a*, *b*) = 5 mm; 2 (*c*) = 5 mm; 3 (*f*, *g*) = 3 mm; 4 (*d*, *e*) = 1 mm.

dorsal ridge, stronger on right than on left; fingers longer than palm, spooned at tips, prehensile edges close fitting, entire, but small basal tooth of fixed finger opposed by notch in prehensile edge of dactyl.

Walking legs rather long, first walking leg (Fig. 8*g*) reaching almost to tip of chela, second and third reaching about to base of dactyl on preceding leg; corresponding articles of respective legs approximately equal in length except for meri which decrease posteriorly; each merus with rounded, rugose dorsal crest ending in distal spine; each carpus with longitudinal dorsal and dorsolateral rib ending in more or less well-developed spine, and often with secondary spine(s) on distal margin between them; each propodus slender, bearing small movable spine distolaterally at base of dactyl; each dactyl slender, acute corneous tip preceded by row of 12 or more movable spines on prehensile edge. Slender fifth leg with well-developed cleaning brush on more or less flattened dactyl opposed by similar setae on distal end of propodus.

Variation.—There is minor variation in ornamentation of the specimens available for study, but none of it is associated with the disjunct distribution in the Golfo de California and the northeastern Pacific.

Remarks.—The specimens reported here were taken around hydrothermal vent sites discussed by Canadian American Seamount Expedition (1985), ASHES Expedition (1986), and Tunnicliffe et al. (1985, 1986). *Munidopsis* has been sighted at three other sites along Juan de Fuca Ridge, but the only specimens collected are those listed above (V. Tunnicliffe[2]).

Comparisons of *Munidopsis alvisca* with previously described species of the genus are aided by reference to A. Milne Edwards (1880), Milne Edwards and Bouvier (1897), Chace (1942), Sivertsen and Holthuis (1956), and Ambler (1980). Lack of epipods on the pereopods immediately separates *M. alvisca* from species such as *M. crassa* Smith, 1885 and *M. subsquamosa* Henderson, 1885 which it superficially resembles. Both of the latter species have relatively prominent rugae and spines on the cephalothorax and legs whereas *M. alvisca* has fairly smooth ornamentation on these body parts, except for minor development of spines on the lateral carapace margin anteriorly. The rostrum of all of these species is narrowly triangular, curves moderately upward to the tip and bears a middorsal carina, but the carina in *M. alvisca* bears almost imperceptible scalelike rugae and diminishes to obsolescence on the gastric region whereas in both *M. crassa* and *M. subsquamosa* the carina is varyingly rugose, rather strongly so in the former, and maintains this ornamentation onto the gastric region. Moreover, *M. crassa* bears tiny irregular marginal spines on the rostrum.

Spination of the merus of the third maxilliped is far weaker in *M. alvisca* than in the other two species discussed, and both the anterolateral spine of the ischium and the crenulate margin of the crest on the ischium are less developed than in them. On the other hand, *M. alvisca* possesses both mesiodorsal and mesioventral eye spines whereas *M. subsquamosa* and *M. crassa* lack the mesioventral spine.

More distant comparisons seem inappropriate because of different body proportions and ornamentation, rostral width, length, elevation and spination, and structure of the eye and third maxilliped. The keys for identification by both Chace (1942) and Pequegnat and Pequegnat (1970), for example, though strictly applicable to species of the Atlantic basin, would ally *M. alvisca* with *M. aries* (A. Milne Edwards, 1880), a much larger species with broader cephalothorax and rostrum, eyes almost hidden from dorsal view, and with less transverse ornamentation. The revised version of this key by Pequegnat and Pequegnat (1971) would place *M. alvisca* in the couplet space occupied by *M. sundi* Sivertsen and Holthuis, 1956, a species with superficially similar shaped cephalothorax, but densely clothed with short setae.

Etymology.—The name is an acronym taken from names of the deep submersible vessels used in collecting the species, *Alvin* and *Pisces IV*.

BRACHYURA: BYTHOGRAEIDAE

Bythograea mesatlantica new species

Figures 9, 10

Material.—USNM 234300, Holotype ♀, Mid-Atlantic Rift Valley about 70 km south of Kane

[2]Verena Tunnicliffe, Department of Biology, University of Victoria, P.O. Box 1700, Victor, B.C., Canada V8W 2R2, pers. commun. 1987.

Fracture Zone (see: Kong et al. [1985]; Leg 106 Shipboard Scientific Party [1986]; Ocean Drilling Program Leg 106 Scientific Party [1986]), 23°22.09'N, 44°57.12'W, 3,437 m, *Alvin* Dive 1683, MARK vent, Stn. 1, scoop, 30 May 1986, pilot D. Foster, observers S. Humphris and J. Edmond. From NSF-Leg 106-Ocean Drilling Program, NSF Grant OEC-8311201 to J. F. Grassle, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—

Carapace		
Length	13.8	
Width	23.3	
Depth of cephalothorax	8.1	
Frontoorbital width	7.7	
Propodus lower margin	R 15.5	L 15.2
Dactyl length	8.3	8.3
Palm		
Height	7.9	7.8
Thickness	4.9	5.1

Description.—General aspect similar to that of *B. thermydron*, cancroid, depressed. Carapace (Figs. 9, 10*d*) broad, transversely elliptical, its rounded lateral angles displaced somewhat anteriorly; almost flat in middle dorsally, very slightly arched from anterior to posterior and near lateral margins; anterolateral region produced, margin not toothed; surface finely granulate anteriorly and laterally, smooth but minutely punctate to unaided eye over posterior 2/3 to 3/4; regions indistinct. Frontoorbital width ca 1/3 carapace width.

Front almost evenly rounded and somewhat deflexed, projecting over folded antennules, shallow median depression continued onto protogastric region giving faint suggestion of bilobation; margin beaded with line of fairly uniform granules, closely packed on anterior and anterolateral parts but diminishing almost to obsolescence near orbits. Arcuate tract of scattered punctations sweeping across anterolateral, hepatic, orbital, protogastric, and metagastric regions. Transverse tract of rather prominent granules at rear edge of protogastric region. Carapace with smooth part behind these anterior areas microscopically granular and punctate anteriorly, grading posteriorly into almost featureless sur-

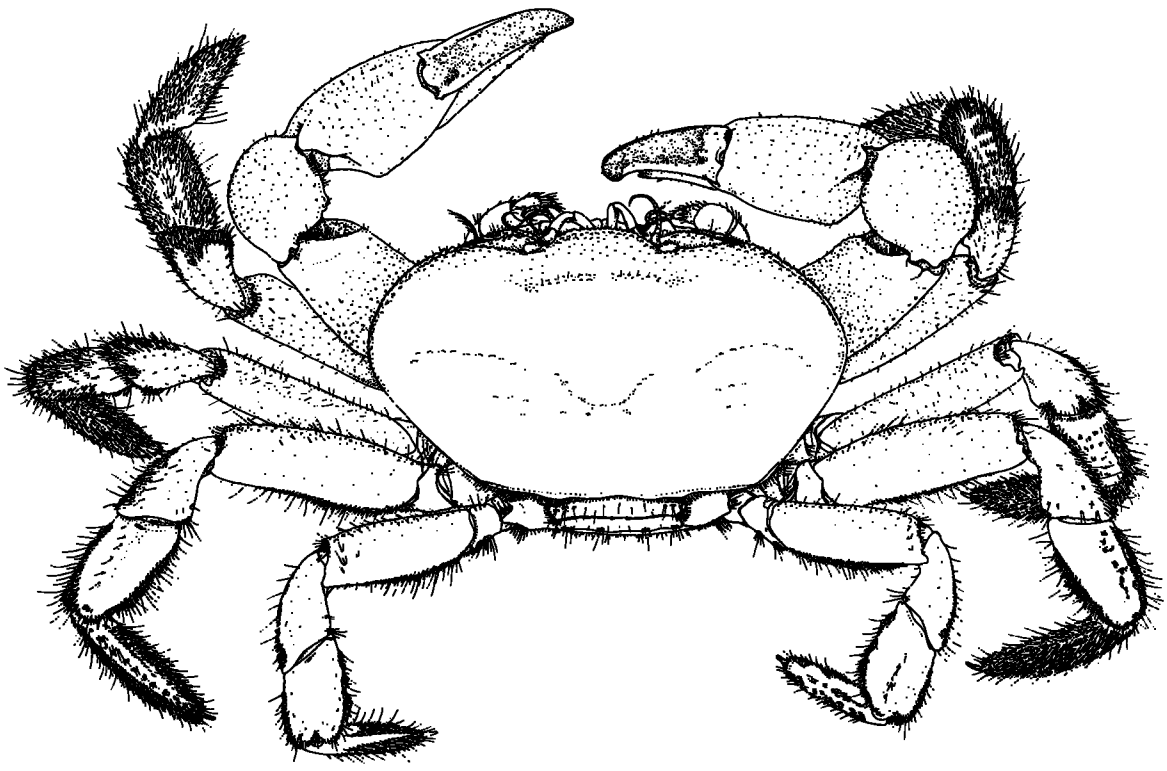

FIGURE 9.—*Bythograea mesatlantica*, holotype ♀: dorsal. Scale = 3 mm.

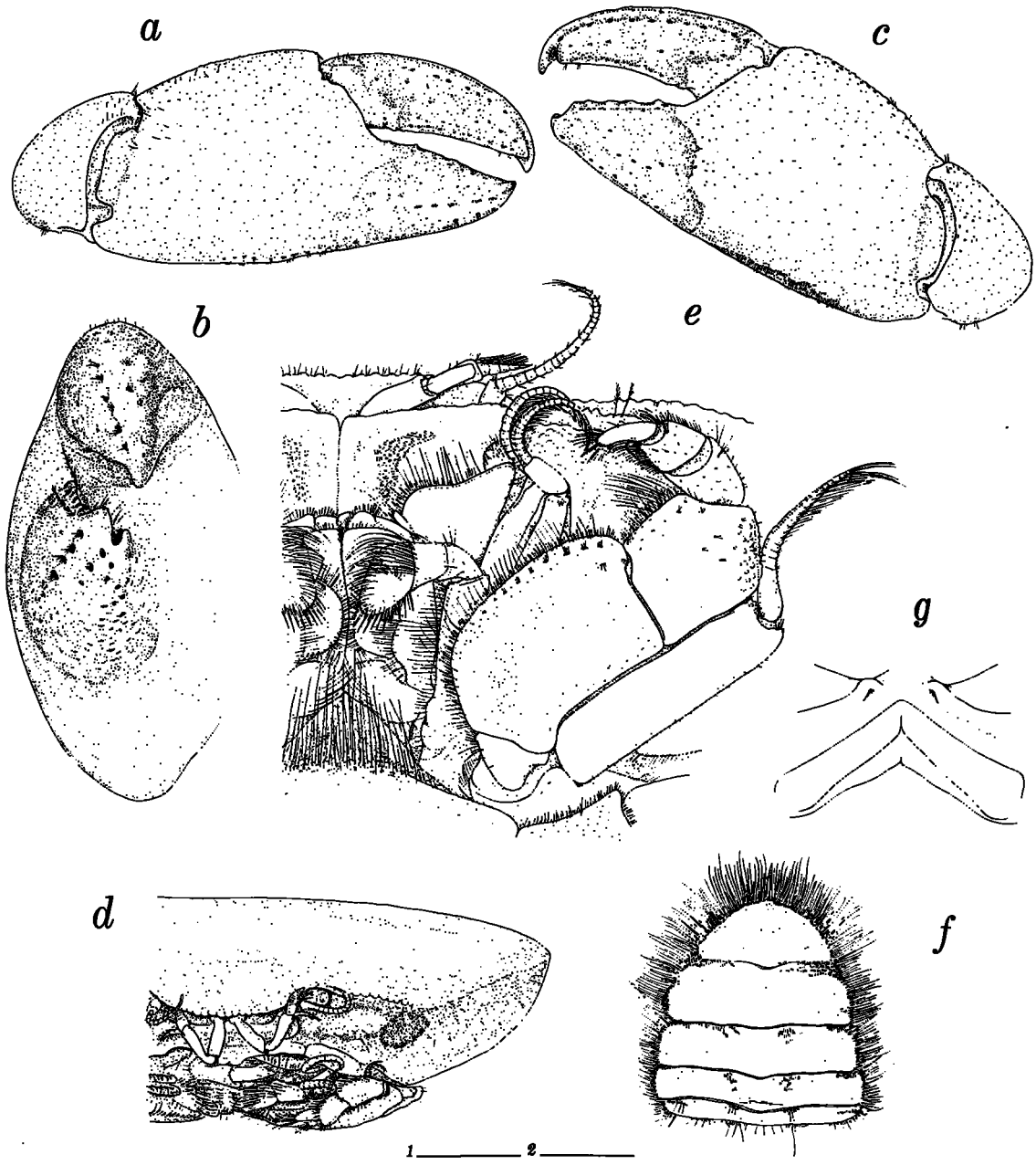

FIGURE 10.—*Bythograea mesatlantica*, holotype ♀: right chela, *a* frontal view, *b* fingers viewed from tips; *c* left chela, frontal view; *d* left side of cephalothorax in frontal view showing anterolateral pigmented spot, eye, antennules, antennae, and mouthparts in situ; *e* mouth field showing third maxilliped turned to side, second maxilliped, first maxilliped with lacinia bearing tiny "portunid lobe" at its mesial corner, partly hidden mandibles, and palate with patch of fine setae to either side of midline; *f* abdomen showing somites 3–6 and telson; *g* oviducal openings and parts of associated sternites. Scales: 1 (*a–d*, *f–g*) = 2 mm; 2 (*e*) = 1 mm.

face. Protogastric, mesogastric, metagastric, and cardiac regions poorly indicated; epibranchial line indicated by small, light colored blotches originating posterior to lateral angle at each side and arching anteromesially over branchial region, then posteromesially toward mesogastric region. Posterior margin concave and paralleled by obsolescent postmarginal groove becoming more pronounced along posterolateral margin.

Subhepatic and subbranchial areas ornamented with small granules, coarsest along upper part of hepatic region but becoming finer and more numerous near base of chelipeds.

Orbits sunk into essentially smooth transverse concavity in anterolateral region confluent laterally at either side with a prominent irregularly oval tan colored spot having very finely granulate, shallowly concave surface; somewhat inflated and irregularly granular suborbital area almost fully visible in dorsal view, reaching level of front, tilted anteroventrally from frontal plane lateral to and almost at same level as epistome.

Eyestalks projecting anterolaterad, barely movable, depressed and broadened to fit snugly in orbit; unpigmented cornea terminal, subcircular, narrower than eyestalk and anterolaterally oriented.

Epistome (Fig. 10*e*) projecting well beyond front, its anterior margin cut into 6 unequal lobes; rather narrow and advanced submedian lobes, separated by narrow deep notch, much broader intermediate lobes and somewhat less broadened lateral lobes less advanced.

Antennules folding transversely, stouter than antennae, large bulbous basal articles contiguous, concealed beneath front, interantennular septum represented by minute remnant at upper and lower edge of antennular fossa; slender penultimate and terminal articles of peduncle nearly equal in length, former slightly hollowed laterally, latter slightly longer and more slender. Flagella short; mesial 7-segmented ramus slender; slightly shorter lateral ramus curved, multisegmented, thick at base but tapering to point, dense mesial brush of long sensory setae in chord of curve.

Antennal insertion mesial to eyestalk; peduncle mesial to eyestalk, extending anteriorly or anterolaterally in situ; fixed article broad but short; first free article slender, ca 1.7 length of second article; latter broadened distally; terminal article short, its diameter only slightly greater than that of flagellar base; flagellar length exceeding midline of front.

Mouth field (Fig. 10*e*) divergent anteriorly, sides of its frame broadest posteriorly and somewhat swollen and granular at anterolateral corners, maximal inside anterior width about 1.4 minimal inside posterior width. Third maxillipeds filling mouth field except for narrow gap of nearly uniform width between ischia of endognaths and rather irregular gap anteriorly between meri-carpi of endognaths and epistome; exognaths overlapping sides of mouth frame. Endognaths with exposed surface bearing sparse, sometimes linear, setose punctations; exposed surface of ischium nearly smooth; elongate polygonal in outline but primarily rectangular, greatest (distal) width 1.1 narrowed part ca 1/2 length from base; mesial margin straight through most of its length but curved at each end, toothless, bearing many stiff straight setae, submarginal zone somewhat thickened and flanked laterally by shallow longitudinal groove; anterior margin nearly perpendicular to mesial margin except for anteriorly projecting truncate lobe at inner corner; lateral margin concave; posteromesial margin obliquely convex; basi-ischial suture line visible posterolaterally. Merus slightly narrower than ischium; low granules with tips directed anteromesially along distal margin; irregularly quadrate perimeter flanked by submarginal thickened zone and groove similar to mesial counterpart on ischium except on straight proximal side, anterolateral angle broadly rounded, anteromesial angle at insertion of palp oblique; mesial margin doubled anteriorly for reception of folded palp, its ventral (exposed) side broadly angled proximal to carpopropodal articulation; posteromesial corner fitted to projecting lobe of ischium, dorsal (hidden) side produced behind carpus, its margin setose. Palp large, dactyl reaching posteriorly about 1/4 length mesial margin of ischium. Carpus expanded distally, narrowed proximally, bent nearly at right angle near insertion and obscurely crimped inside angle; dense tuft of setae on distooral surface. Propodus wider than carpus, longer than broad, asymmetrically ovate in ventral view; distal (longest) margin convex, densely beset with rows of strong serrated setae, longest distally; distal tuft of such setae on dorsal surface. Linear dactyl slightly bent away from midline in distal part and setose as propodus, especially on prehensile edge. Exognath narrow, not extending to full length of merus; ventral surface slightly curved mesially to fit closely against lateral side of endognathal ischium, with dorsomesial flange (widest distally)

fitting beneath latter; palp conspicuous, flagellum densely beset with setae in hollow of curve.

First maxilliped with lacinia of endopod broad, its distal edge 3-lobed and conspicuously though not heavily setose; oblique mesial margin of strongly advanced anterolateral lobe confluent with broader gradually rounded and much less advanced intermediate lobe, latter in turn followed by still less advanced tiny mesial lobe, separated by a notch and directed anteromesially; tuft of setae preceding notch.

Endostome large, divided by low median sagittal ridge bifurcated somewhat anteriorly and merging into projecting endostome; each half of palate shallowly concave, crossed by low longitudinal ridge slightly offset at its midlength and trending anteromesially from near base of large mandibular palp; ridge flanked laterally by irregular patch of velvety pubescence; smooth lateral 2/3 of palate receiving large efferent branchial channels.

Chelipeds (Figs. 9, 10*a*, *b*, *c*) heavy, subequal; integument punctuate on upper and extensor surfaces, obscure granulation on upper surfaces of palms and on ridges or raised areas elsewhere; chelae inflated, lower margin of palm arched downward, its rather pronounced keel merging into fixed finger; swollen palm with shallow excavation proximally for reception of carpus in flexed position, inner surface glabrous but drawn into moderate and slightly granular elevation slightly in front of proximal excavation. Fingers tan colored in preservation (70% ethanol) and darkest proximally, color of fixed finger not extending onto palm; fingers not gaping, prehensile edges entire except for obsolescent proximal tooth on fixed finger of each hand; dactyl longer than relatively straight fixed finger, arching down distally to close in distal notch of spooned tip of fixed finger.

Carpus with extensor surface inflated, right carpus with internal margin rounded, that of left obscurely angled. Merus broadened mesially into cristate flange angled distally for reception of carpus, strong granules in single line along inner margin, outer surface rounded, strewn with obsolescent punctations and granules, latter most prominent along distoventral tract.

Walking legs rather long, flattened, length decreasing posteriorly in order 3, 2, 1, 4; each with dense patches of short darkened setae interspersed with sparer longer setae on extensor surface of carpus and propodus (as well as its lateral side on legs 1 and 2), distoventral corner of carpus, and more extensively on dactyl; fifth legs somewhat more flattened than others, propodi relatively broader and not densely setose laterally. Mean maximum length of propodi about twice width. Dactyls slightly longer than propodi, narrowly lanceolate, shallow longitudinal grooves on anterior and posterior surfaces obscured by dense setae, tip stout, corneous. Merus of each with upper margin finely granular, anterior lower margin present throughout length but posterior lower margin obsolescent proximally.

Sternum broadest between legs 1 and 2, narrower posteriorly, glabrous beyond outline of abdomen.

Abdomen (Fig. 10*f*) ovate in outline, fully segmented and densely fringed with plumose setae; somite 1 slightly arched dorsally to fit contour of adjacent carapace, somites 2–4 of about equal length, somites 5 and 6 progressively longer; abdomen with greatest width at 4; telson nearly as broad as somite 6, outline broadly arched distally. Somites 2–5 bearing large, well-developed biramous pleopods, outer curved branch lying near edge of abdomen and heavily beset with short setae laterally and mesially, inner branch more sparsely equipped with ovigerous setae and jointed.

Female openings (Fig. 10*g*) large, obscurely subtriangular in outline.

Color in preservation predominantly off-white except for fingers, matted setal tracts laden with brownish finely particulate matter.

Remarks.—Brachyuran crabs that resemble *Bythograea* were observed and reported by Rona et al. (1986).

Bythograea mesatlantica differs in several respects from Pacific members of the genus, *B. thermydron* Williams (1980) and *B. microps* de Saint Laurent (1984). Among obvious differences from *B. thermydron*, the new species has even less ornamentation on the carapace; it lacks a distinct suborbital plate separated by a suture, and the suborbital area is inflated, not flat and inclined; there is a transverse concavity lateral to each eyestalk that terminates near the very distinctive brown spot in the cuticle at either side of the carapace; the eyestalk itself is shorter and thicker than in *B. thermydron* and the shape and position of the cornea differs. The ischium of the third maxilliped is relatively shorter than in *B. thermydron* and bears only sparse setiferous punctations on the external surface, it lacks tiny granules on the truncate lobe at the anterolateral

corner, the submarginal thickened zone and groove are less distinct; the merus is not tilted dorsally in normal position, and the palp is relatively shorter and club shaped rather than curved like a knife edge along the prehensile edge. The lacinia of the first maxilliped is more angular anterolaterally and has a smaller "portunid lobe". The epistome is less lobulate than in *B. thermydron* and the concave palatal area has much less setose covering. The nearly toothless chelae have brown fingers and there is no dense patch of setae on the inner side of the palms.

Comparisons with *B. microps* are necessarily less complete because of the brief description of the latter. The eyes are certainly not slender and retracted in *B. mesatlantica*; the chelipeds are not noticeably dimorphic, and they are relatively smooth rather than strongly granular and pilose on the external surface as in *B. microps*.

The distinctive exocular spots on the carapace seem similar to those noted on the chelipeds of *Hypsophrys noar* Williams (1974, 1976) and *Munidopsis lentigo* (Williams and Van Dover 1983). Their function is unknown.

Etymology.—From the Greek "mesos", middle and "Atlantic", with reference to the Mid-Atlantic Rift habitat.

ACKNOWLEDGMENTS

Contributors of specimens and crew members of submersible vessels who helped to make the collections are owed a special debt of gratitude for securing the rare material described here. Donors are acknowledged individually in each of the species accounts. I am indebted to Keiko Hiratsuka Moore for rendering the excellent illustrations, to Ruth Gibbons for helping to produce the SEM micrographs, and to F. A. Chace, Jr., R. B. Manning, and B. B. Collette for critical review of the manuscript.

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THE MEGALOPA STAGE OF THE GULF STONE CRAB, *MENIPPE ADINA* WILLIAMS AND FELDER, 1986, WITH A COMPARISON OF MEGALOPAE IN THE GENUS *MENIPPE*

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ABSTRACT

The laboratory-reared megalopa stage of the Gulf stone crab, *Menippe adina*, is described and illustrated and compared with megalopae of three other species of *Menippe*. The megalopa of *M. adina* differs from that of *M. nodifrons* in having serrate spines on the ventral margin of the dactylus of pereiopod 5 and from that of *M. rumphii* in having spines on the dactyli of pereiopods 2–5 and a more quadrate carapace. The megalopa of the morphologically similar *M. mercenaria* was also reared in the laboratory, and selected characters are described and compared with the megalopa of *M. adina*; megalopae of the two species differ only slightly. Megalopae of *M. adina* taken from field collections made off South Texas, U.S.A., were compared with and were found to be consistent with laboratory-reared *M. adina* megalopae.

Stone crabs of the genus *Menippe* are large xanthid crabs common along the eastern coasts of the United States and Mexico from North Carolina to Yucatan, the Bahamas, Cuba, and Jamaica (Rathbun 1930; Felder 1973; Williams 1984; Williams and Felder 1986). Recently the "common" stone crab, *Menippe mercenaria* (Say, 1818), was divided into two species: *Menippe mercenaria* (Say) (restricted), known from the east coast of the United States, the Caribbean, and the west coasts of Florida and Yucatan, and *Menippe adina* Williams and Felder, 1986, known from the northwestern Gulf of Mexico; hybridization of the two species occurs in northwest Florida (see Williams and Felder 1986). These two species (primarily *M. mercenaria*) support an important stone crab fishery in the southern United States and Mexico (Williams and Felder 1986) and consequently have been the subject of numerous investigations. Despite this interest, the complete larval developments of both commercial species of *Menippe* remain unknown. For *M. mercenaria* (Say), Hyman (1925) described a prezoea and first zoeal stage, and Porter (1960) described six zoeal stages reared in the laboratory. Unfortunately, Porter did not describe the megalopa stage, presumably because he considered it a postlarva and not a true larval stage. An unpublished but often-cited report by Kurata[4] included descriptions of the zoeal stages of *M. mercenaria* and a brief sketch of the megalopa; Kurata's description of the megalopa did not include morphology of the pleopods, pereiopods, or mouthparts.

Because of recent interest in the phylogenetic significance of the brachyuran megalopa (see Rice 1981a, in press; Martin in press) and postlarval stages (Martin et al. 1984; Felder et al. 1985), and because of the potential importance of stone crab larval biology to aquaculture, it is surprising that the megalopae of *M. mercenaria* and *M. adina* remain undescribed. The present paper describes the laboratory-reared megalopa of the Gulf stone crab, *Menippe adina* Williams and Felder, and compares it with field collections of the same species from south Texas, laboratory-reared megalopae of *M. mercenaria*, and all previously described megalopae of the genus *Menippe: Menippe mercenaria* (Say, 1818) (as described by Kurata fn. 4); *Menippe nodifrons* Stimpson, 1859 (as described by Scotto 1979); and *Menippe rumphii* (Fabricious, 1798) (as described by Kakati 1977).

MATERIALS AND METHODS

A large ovigerous *M. adina* was collected from

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[4]Kurata, H. 1970. Studies on the life histories of decapod Crustacea of Georgia. Part III. Larvae of decapod Crustacea of Georgia. Unpubl. rep., 274 p. University of Georgia Marine Institute, Sapelo Island, GA.

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shallow waters of the northern Gulf of Mexico near Grande Terre, LA, in May 1982 and held in a small aquarium at room temperature. After the eggs hatched, the zoeal larvae were given fresh seawater and newly hatched *Artemia* nauplii daily. Exuviae as well as dead and some living megalopae were preserved in 70% ethanol. Drawings were made with the aid of a Wild[5] M-5 stereoscope and a Wild M-11 compound stereoscope, both with camera lucida; accuracy was verified with a Nikon Optiphot. Measurements were made with an ocular micrometer. Ten laboratory-reared megalopae were examined, measured, dissected, and compared with megalopae from field collections made in 1973 off south Texas. Comparisons with *M. mercenaria* are based on laboratory-reared *M. mercenaria* megalopae from two females collected on 13 August 1987 from the Indian River system, north of Ft. Pierce, FL. Eggs of these two females hatched on 21 August 1987, and the megalopa stage was first reached after 17 days in mass culture aquaria (30‰ salinity, 25°C, 12h:12h light/dark regime). Descriptions of setation for all appendages proceed from proximal to distal. Specimens examined under the scanning electron microscope (SEM) were prepared according to procedures outlined by Felgenhauer (1987) but without postfixation in osmium tetroxide and with 100% ethanol, rather than amyl acetate, as the transitional fluid. Sibling megalopae and field collections have been deposited in the U.S. National Museum of Natural History, catalogue No. USNM 229962 (laboratory-reared *M. adina*), USNM 229961 (field-collected *M. adina*), and USNM 229963 (laboratory-reared *M. mercenaria*).

RESULTS

Carapace (Figs., 1A, B, C, 3A).—Length 1.67 mm, width 1.45 mm ($N = 10$). Subquadrate, with 2 lateral prominences on each side; dorsoventrally thick, with minute tubercle centrally located. Posterior border fringed with numerous short setae; lateral margin with few scattered setae. Rostrum ventrally deflexed, nearly vertical, with deep medial depression, rounded anteriorly. Angular interorbital prominences extend ventrally between orbit and antennule. Chromatophores variable in placement, but almost always found in areas indicated in Figure 1B.

Eyes (Figs. 1A, B, C, 3A).—Large, exposed; eyestalks sometimes with 2 or 3 short, simple anterior setae, always with posterodorsal chromatophore.

Abdomen (Fig. 1A, B).—Subequal in length to carapace. All pleura with rounded posterolateral angles. All somites with sparse setae dorsally; somites 2–5 always with elongated chromatophores.

Telson (Fig. 1G).—Broadly rounded with variable setation, occasionally with pair of small posterior spines (as in Figure 1B).

Antennule (Fig. 1K).—Biramous; peduncle 3-segmented, with variable setation. Basal segment of peduncle large, bulbous, always with large chromatophore; middle segment subcylindrical with 0–2 distal setae; distal segment ovoid with scattered short setae. Lower ramus 1-segmented with 6–8 setae; upper ramus 5-segmented with aesthetascs arranged in tiers, usually 0, 7, 8, 6, 4 subterminal plus 3 terminal, with short setae sometimes present on segments 2 and 4 (note: all aesthetascs not illustrated).

Antenna (Fig. 1J).—Flagellum 12-segmented (sometimes 11), with 3 peduncular articles and 8 or 9 flagellar articles (see Rice, in press, for correct number of antennal segments in megalopae); setation variable, usually 2, 3, 2, 0, 0, 2, 4, 0, 4 or 5, 1, 4, 4.

Mandibles (Fig. 2F).—Asymmetrical, with broadly rounded spade-shaped cutting edges; palp 2-segmented with setation 0, 11–14.

Maxillule (Fig. 2E).—Protopodite with 1 or 2 long plumose setae on posterodorsal margin; endopodite 2-segmented with setation 1, 2 subterminal plus 2 terminal; basal endite with 29–35 spines and setae; coxal endite with 13–16 spines and setae.

Maxilla (Fig. 2D).—Scaphognathite with 70–78 fringing setae and 0–6 setae on blade; endopodite unsegmented with 0 or 1 distolateral seta and 4 or 5 basal plumose setae; basal endite bilobed with setation variable, usually 8–10, 9–11; coxal endite bilobed with setation usually 7, 9 or 10.

Maxilliped 1 (Fig. 2C).—Exopodite 2-segmented, with setation 2 or 3, 5–7. Endopodite

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

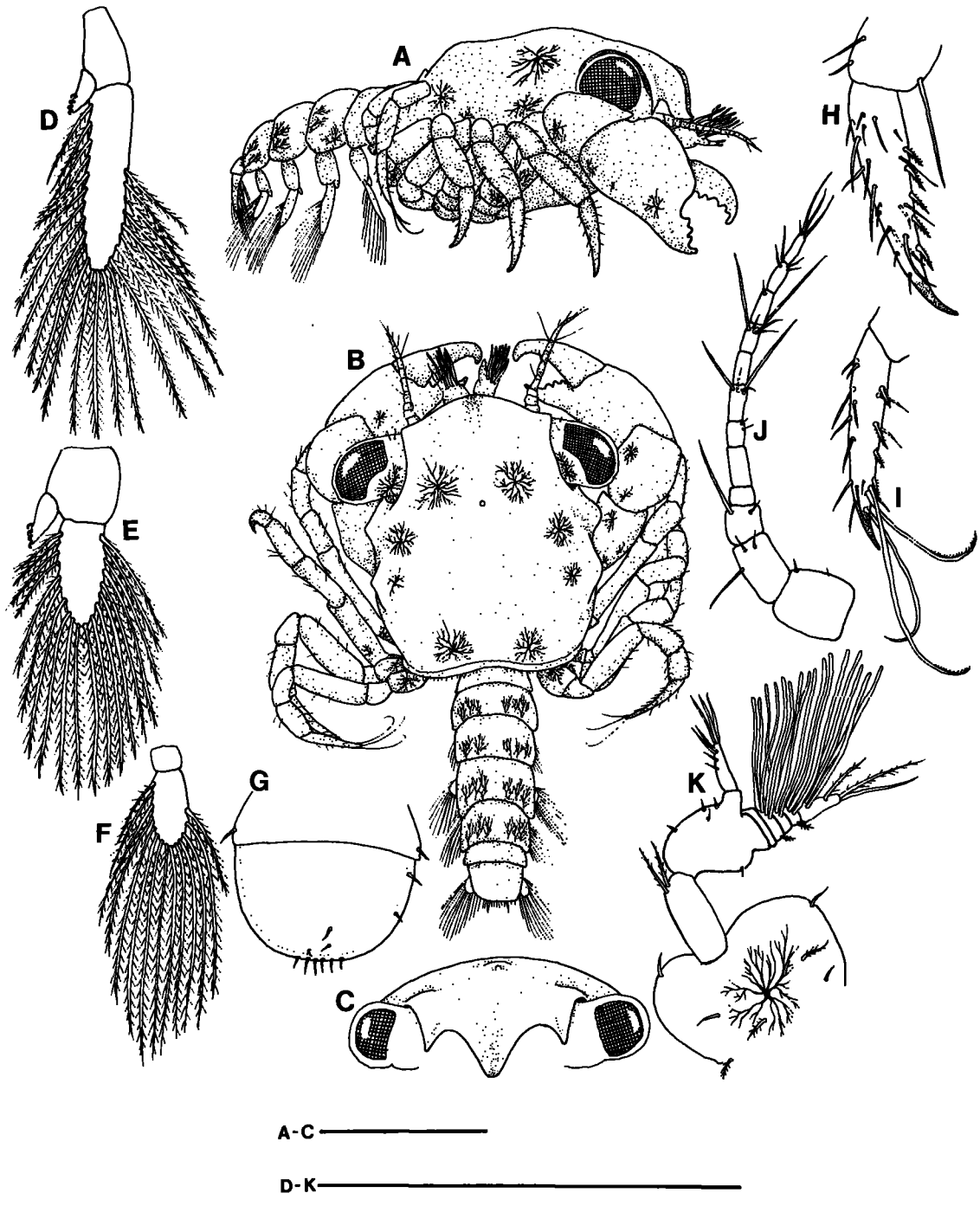

FIGURE 1.—Megalopa of the Gulf stone crab, *Menippe adina*. A, entire animal, lateral view; B, same, dorsal view; C, frontal view of rostrum and eyes; D, pleopod 1; E, pleopod 4; F, pleopod 5; G, telson and posterior part of sixth abdominal segment; H, dactylus of pereiopod 3; I, dactylus of pereiopod 5; J, antenna; K, antennule, Both scale bars = 1.0 mm.

FIGURE 2.—Megalopa of *Menippe adina*, mouthparts. A, third maxilliped; B, second maxilliped; C, first maxilliped; D, maxilla; E, maxillule; F, mandible. Scale bar = 0.5 mm.

unsegmented with 6–8 setae arranged as shown. Basal endite setation 28–33; coxal endite setation 15–17. Epipodite with 22 or 23 long, minutely plumose setae, appearing simple under low magnification.

Maxilliped 2 (Fig. 2B).—Exopodite 2-segmented, with setation 3, 5–8. Endopodite 4-segmented, with setation usually 5, 2 or 3, 5 or 6, 9 or 10; distal segment with 4 or 5 stout serrate setae. Epipodite with 9 or 10 long minutely plumose setae.

Maxilliped 3 (Fig. 2A).—Exopodite 2-segmented, with setation 0 or 1, 6–8. Endopodite 5-segmented, with variable setation, usually 18–20, 15 or 16, 5–9, 6–8, 7–10; ischium with scalloped medial border. Epipodite with 18 long minutely plumose setae on distal two-thirds plus 8–12 plumose setae on proximal one-third. Protopodite setation variable.

Pereiopods (Figs. 1A, B, H, I, 3B, C, D).—Chelipeds long, stout, subequal; dactylus with 4 irregular teeth; immovable finger with 3 teeth (Fig. 3B); tips of fingers overlap distally when approximated. No recurved hook on basi-ischium (Fig. 3B). Second to fourth pereiopods similar; dactylus with 5 (rarely 4) serrate spines ventrally (e.g., Figs. 1H, 3C, D); propodus with long ventrodistal spine (Fig. 1H). Fifth pereiopod dactylus (Fig. 1I) with 3 long pectinate setae, 1 markedly toothed and concave (Fig. 3E), on distal ventral border and 3 or 4 serrate spines ventrally.

Pleopods (Fig. 1D, E, F).—Decreasing in size posteriorly. Pleopod 1 (Fig. 1D) with 19–22 plumose setae; endopodite with 3 or 4 hooked setae. Pleopod 4 (Fig. 1E) with 19–21 plumose setae; endopodite with 3 or 4 hooked setae (Fig. 3F). Pleopod 5 (uropod) (Fig. 1F) with 12–14 plumose setae; basal segment lacking setae or with 1 or 2 setae (field collections); endopodite absent.

Color.—Overall coloration rose-orange, with dark blue-black chromatophores located as shown in Figure 1A, B.

DISCUSSION

The genus *Menippe* de Haan, 1833, presently contains about 8 species, only 3 of which occur in North America. The megalopa stage is now known for 3 species in the genus: *M. rumphii* (Fabricious, 1798), *M. nodifrons* Stimpson, 1859, and *M. adina* Williams and Felder, 1986. In addition, selected characters of *M. mercenaria* (Say, 1818) are presented here for comparison; some characters of that species are also obtainable from an unpublished report by Kurata (fn. 4) (see Table 1).

Laboratory-reared megalopae of *M. adina* were virtually identical to megalopae presumed to belong to *M. adina* that were collected off south Texas. Even meristic counts of the mouthpart setation agreed exactly, with the only observed differences being that field-collected megalopae were slightly larger and occasionally bore 1 or 2 setae on the basal segment of the uropod. Thus, we feel that our laboratory conditions have not adversely affected development or introduced abnormal characters, and we have used these field collections for the SEM figures of *M. adina* megalopae (Fig. 3).

We expected to find that characters of the megalopa of *M. adina* are similar to those described by Kurata (fn. 4) for the morphologically similar (in adulthood) *M. mercenaria*, a species known to hybridize with *M. adina* (see Williams and Felder 1986). In general this is true. However, some characters reported by Kurata differ from our observations on *M. adina* and from our laboratory-reared megalopae of *M. mercenaria* (Fig. 4). Kurata mentioned (but did not illustrate)

TABLE 1.—Comparison of characters in megalopae of the genus *Menippe*. Dash (—) indicates information not available from reference.

	Size[1] (mm)		Setation				Spination			
				Epipod of			Dactylus of			
Menippe	CL	CW	Palp of mandible	Maxilliped 1	Maxilliped 2	Maxilliped 3	Pereiopods 2–4	Pereiopod 5	Setation pleopod 5	Reference
adina	1.67	1.45	0, 11–14	22–23	9–10	18	5	4	12–13	Present study
mercenaria	1.70	1.55	0, 11–13	20–23	7–10	18–20	4	4	11–13	Present study
mercenaria	1.7–8	—	—	—	—	—	4–5	0	11–12	Kurata[3]
nodifrons	1.50	1.31	0, 10–13	12–20, [2]26	up to 10	18	5	0	11	Scotto 1979
rumphii	1.60	1.55	0, 0, 9	22	8	18	0	0	12	Kakati 1977

[1]CL = carapace length; CW = carapace width.
[2]From a megalops hatched from a stage 6 (rather than the typical stage 5) zoea.
[3]See text footnote 4.

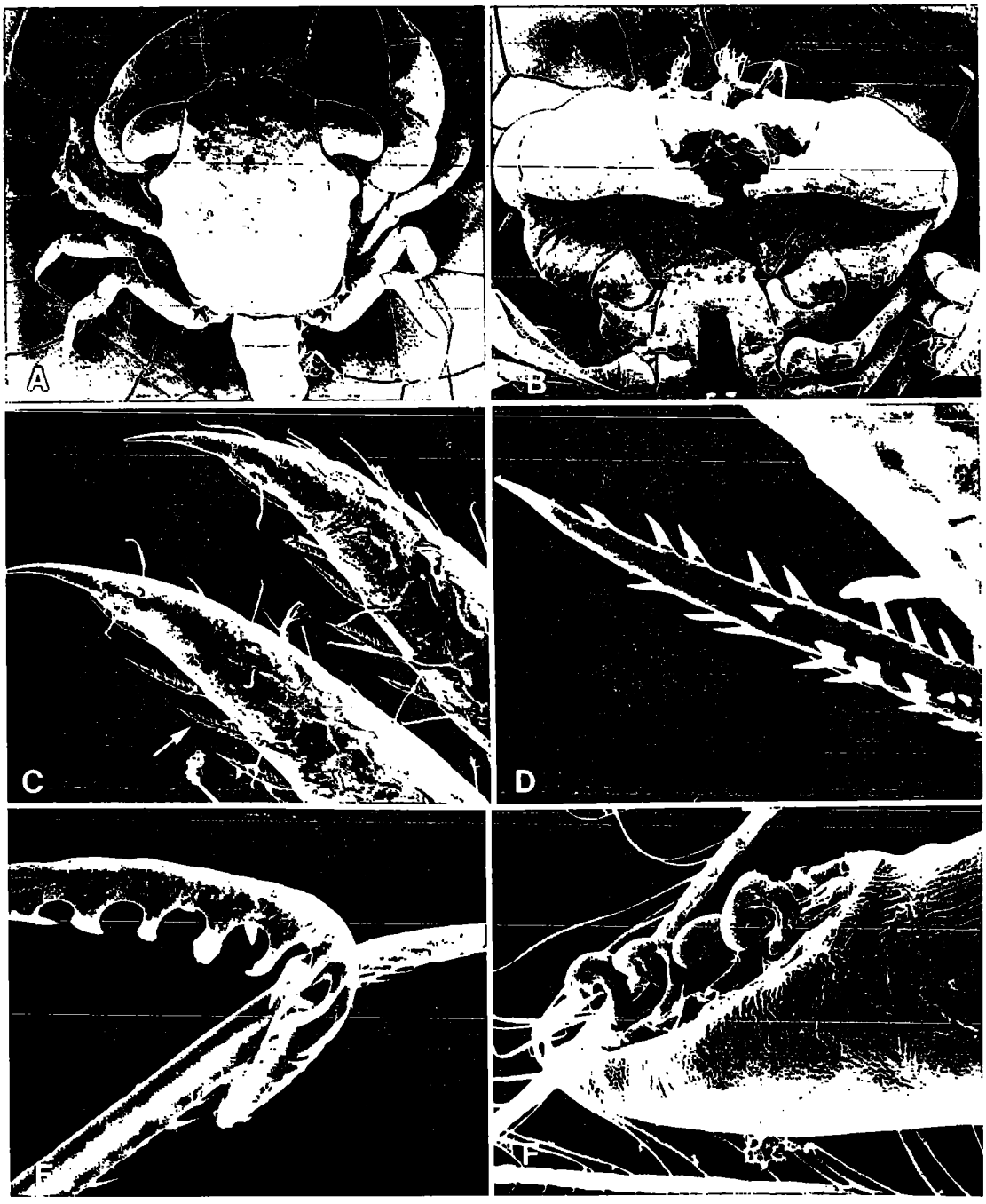

FIGURE 3.—Scanning electron micrographs (SEM) of selected characters of *Menippe* megalopae (presumably *M. adina*) collected in south Texas. A, dorsal view of carapace (× 25); B, ventral view of chelipeds showing dentition of the fingers and lack of recurved hook on ischium (× 37); C, dactyli of second (upper figure) and third pereiopods (× 230); D, higher magnification of ventral dactylar spine indicated by arrow in C (× 1,900); E, endopod of third abdominal pleopod showing 4 dentate hooklike setae (× 2,200); F, serrate setae (only 2 of 3 shown) of dactylus of pereiopod 5 (× 2,300).

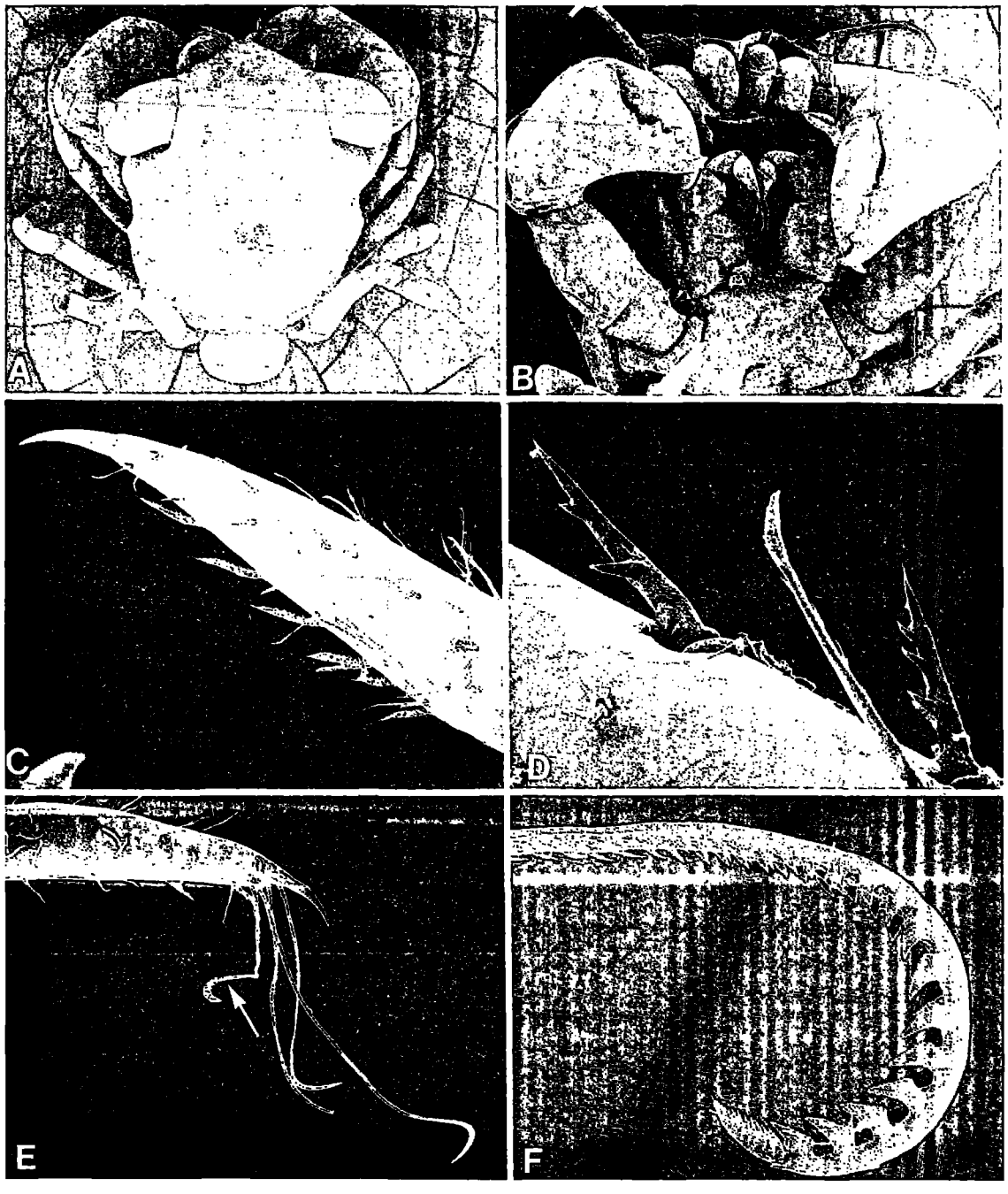

FIGURE 4.—Scanning electron micrographs (SEM) of selected characters of the laboratory-reared megalopa of *Menippe mercenaria*. A, dorsal view of carapace (× 37); B, ventral view of chelipeds and third maxillipeds (× 55); C, dactylus of second pereiopod showing ventral serrate spines (× 270); D, ventral spines on dactylus of fourth pereiopod with fewer spinules than anterior pereiopod spines (× 2,000); E, dactylus of fifth pereiopod showing four serrate "sensory" setae with one (arrow) more obviously serrate (× 190); F, higher magnification of concave serrate setae indicated by arrow in E (× 1,500).

"about 9 small spines" on the ischium of the third maxilliped; we found no spines on *M. adina* or *M. mercenaria* (Figs. 3B, 4B), but it is possible that Kurata was referring to the acute borders of the scalloped medial margin (our Figure 2A), in which case the 2 species are similar. Spination of the ischium of pereiopods 1–3 differs also; Kurata described 5 or 6, 2 or 3, and 1 small spine on the ischia of pereiopods 1, 2, and 3, respectively, whereas we did not notice this condition in *M. adina* or *M. mercenaria* (see Figures 3B, 4B). Finally, Kurata (fn. 4: pl. 74, fig. E) illustrated no spines on the ventral surface of the fifth pereiopod dactylus of *M. mercenaria*; these spines are obvious on both species (Figs. 1I, 4E). We found few differences between megalopae of *M. adina* and *M. mercenaria*. General morphology of the carapace and chelipeds, spination of the dactylus of the pereiopods, and setation of the pleopods agreed almost exactly (compare Figures 3 and 4). Ventral dactylar spines on the posterior walking legs of *M. mercenaria* were not so serrate as in *M. adina* and were sometimes armed with only 2 or 3 large spinules rather than the numerous spinules seen in *M. adina* (e.g., Fig. 3D) and in the more anterior legs of *M. mercenaria* (see Figure 3C, D, 4C). Also, in all but 1 of the 9 megalopae of *M. mercenaria* examined there were 4 (rather than 3) long serrate setae on the dactylus of the fifth pereiopod (Fig. 4E). As in *M. adina*, one of these setae was more serrate and concave than were the other long setae (Fig. 4E, F). However, we have not examined mouthpart morphology of *M. mercenaria* in the detail in which we described *M. adina*, and so it is possible that additional characters will be found to separate these 2 species at the megalopa stage.

The megalopa of *M. adina* is very similar to that of *M. nodifrons* as described by Scotto (1979). Although the 2 species differ in setation of some of the mouthparts, this setation may differ from side to side in a given individual. The salient character that serves to separate megalopae of these 2 species is the presence in *M. adina* of 4 stout serrate spines on the dactylus of pereiopod 5. Scotto (1979) figured only setae (and no spines) on the dactylus of the fifth pereiopod in *M. nodifrons* and the dactylar spines on other pereiopods apparently are not serrate (Scotto 1979, fig. 9c, pereiopod 3).

The megalopa of *M. rumphii* described by Kakati (1977) differs from that of *M. nodifrons*, *M. mercenaria*, and *M. adina* in having a more ovoid carapace with the rostrum only slightly deflexed. Kakati did not describe the dactyli of pereiopods 2–5 for *M. rumphii*, but his figure of pereiopod 2 (1977:639, fig. 2, p. 50) does not show stout ventral spines on the dactylus. Possibly Kakati overlooked these spines; if not, the absence of these spines on pereiopod 2 would further serve to separate the megalopa of *M. rumphii* from those of *M. nodifrons*, *M. mercenaria*, and *M. adina*. All 4 species have been described as having a rose-orange coloration in life.

Although Rathbun (1930) and Monod (1956) synonymized *M. rumphii* with *M. nodifrons*, descriptions of the zoeal stages of *M. rumphii* and *M. nodifrons* by Kakati (1977) and Scotto (1979), respectively, show that larvae of the 2 species differ considerably. In the first zoeal stage, *M. rumphii* exhibits elongated posterolateral processes on abdominal segment 5 that extend posteriorly to more than half the length of the telsonal furcae, which lack spines. The first zoea of *M. nodifrons* has similar posterolateral processes but these do not extend posteriorly beyond the fork of the telson; the telsonal furcae bear 1 dorsal and 2 lateral spines each. These differences are not apparent in later zoeal stages, but their presence in the first zoeal stage and the differences noted in the megalopa stage may be reason to question the synonymy of these 2 species.

Xanthid larvae are known to be variable, and it is often difficult to reconcile larval and adult groupings based on morphology. Larvae of some morphologically disparate (as adult) species are very similar, whereas zoeal stages for species in some genera differ markedly in their morphology (see Martin 1984; Martin et al. 1984, 1985; Martin and Abelé 1986). Because of the known morphological variability of xanthid larvae, characters presented for taxonomic purposes here and elsewhere (e.g., Martin 1984) must be used with caution.

It is not our intent to promote descriptions of single stages in the life cycles of brachyuran crabs. However, in those cases where a description of a single stage adds appreciably to our knowledge of phylogeny (e.g., Rice 1981b) or fills a gap in the larval biology of a commercially important species complex (present study), we feel such a description is justified. A detailed comparison of zoeal stages of the two species is planned for the near future.

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OCEANOGRAPHIC ASSOCIATIONS OF NEUSTONIC LARVAL AND JUVENILE FISHES AND DUNGENESS CRAB MEGALOPAE OFF OREGON

JONATHAN M. SHENKER[1]

ABSTRACT

The larval and juvenile fishes and crabs inhabiting the neustonic zone within 50 km of the coast were sampled biweekly from April through July 1984, with a Manta net (mouth 1.0 m wide × 0.7 m deep), and a large neuston trawl (mouth 3.5 m wide × 1.0 m deep). The Manta net was an efficient sampler for larval fishes and crabs, while the neuston trawl collected larger juvenile fishes that had rarely been observed in previous studies.

Nocturnal sampling accounted for nearly all the ichthyoneuston and zooplankton taken. Dungeness crab megalopae were the most abundant species. Although present throughout the survey, the great majority were found in very large aggregations along visible convergence zones or in association with *Velella velella*. Discrete groups of abundant larval and juvenile fishes were found prior to upwelling (*Parophrys vetulus*, *Scorpaenichthys marmoratus*, *Hemilepidotus spinosus*, *Hexagrammos* sp., and *Anoplopoma fimbria*) and after its onset (*Engraulis mordax* and *Sebastes* spp.). These species had distinct zonal (east-west) distribution patterns and were generally associated with, or affected by, hydrographic characteristics such as convergences, upwelling, and the Columbia River plume.

Recent studies of the ichthyoplankton off the northwest coast of the United States have contributed new information on the temporal and spatial occurrences of larvae of coastal and pelagic fish species (Richardson 1973; Richardson and Pearcy 1977; Laroche and Richardson 1979; Richardson et al. 1980; Kendall and Clark 1982a, b; Clark 1984; Bates 1984; Mundy 1983; Brodeur et al. 1985; Boehlert et al. 1985). These surveys focused on larvae occurring below the surface layer of the ocean, although concurrent neustonic samples were occasionally collected (Kendall and Clark 1982 a, b; Clark 1984; Bates 1984; Richardson[2]). Comparison of simultaneous surface and subsurface samples demonstrated that many species were found in both depth strata, while an additional group of species was collected only from the neustonic zone. Brodeur et al. (1987) examined the larval fish and invertebrate components of the neuston in the northeast Pacific, and determined that these organisms were frequent prey items of juvenile salmonids.

Standard plankton and neuston nets used in these studies were effective in collecting the relatively slow-moving early larvae. However, net avoidance by larger larvae and juvenile stages (Barkley 1972; Murphy and Clutter 1972) suggests that use of traditional collecting gear is inappropriate for more mobile fishes. This paper describes the results of a neustonic survey conducted off the Oregon coast in the spring and summer of 1984 that focused on the larger ichthyoneuston. Conventional sampling gear and a new net designed specifically for sampling juvenile fishes were used to characterize the temporal and spatial distribution patterns of both larval and juvenile ichthyoneuston and Dungeness crab, *Cancer magister*, megalopae.

MATERIALS AND METHODS

Sampling was conducted at approximately 2-wk intervals from early April through July 1984, on an east-west transect along the 44°40'N parallel, 3 km north of Newport, OR (Fig. 1). Stations were located at distances of 1, 5, 10, 15, 20, 30, 40, and 50 km from shore. The stations were occupied twice during each 24-h cruise, once during the day and once at night. On one cruise (8–10 June), the 50 km station was occupied for 27 hours to assess diel variation in abundance of neustonic organisms. In response to several

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[2]Richardson, S. L. Oregon's coastal ichthyoneuston - a preliminary report. Unpubl. rep. Presented at American Society of Ichthyologists and Herpetologists, Williamsburg, VA, June 1975.

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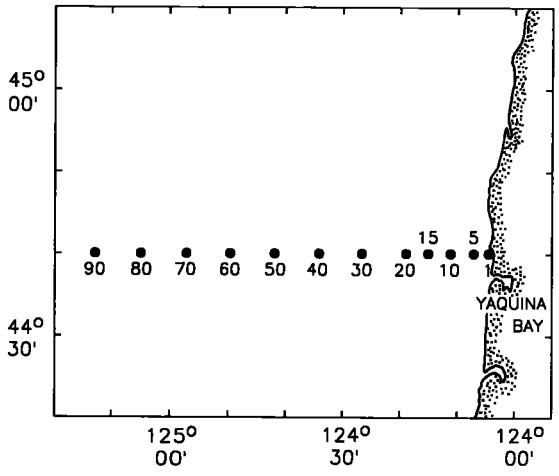

FIGURE 1.—Location of stations along the transect off Newport, OR. The numbers indicate distance offshore in kilometers.

weeks of strong upwelling, during which very few larvae were collected close to the coast, the sampling scheme was modified for the two July cruises by eliminating some of the inshore stations and extending the transect as far offshore as 90 km. Only night samples were collected during July.

One of the primary considerations of the survey was to collect samples while minimizing net avoidance by the target organisms. Reduction of vessel-induced disturbance was accomplished by deploying the collecting gear from the ends of 12 m-long outriggers on the FV *Cumberland Trail*, a chartered 23 m commercial scallop-fishing vessel.

Two different nets were used to collect the samples. Larval fish and zooplankton were collected with a Manta neuston net (Brown and Cheng 1981), modified to have a mouth 1.0 m wide × 0.7 m deep. The Manta frame was equipped with a green-colored 0.333 mm mesh net, PVC cod end bucket, and General Oceanics model 2030 digital flowmeter[3]. A two-point bridle was attached to the upper corners of the frame. Drag on the net while towing kept the entire bridle and towing wire assembly out of the water.

The second net was designed to collect the larger juvenile fishes that were assumed to avoid the smaller Manta net. The neuston trawl was constructed with a mouth 3.50 m wide × 1.05 m deep (Fig. 2a). The frame consisted of 43 mm (outside diameter) heavy-duty galvanized pipe, with towing points welded at the four corners. Flotation for the frame was provided by three inflatable spar buoy floats. These 40 cm diameter floats had hollow tubes running through their centers and were fitted onto the upper bar of the frame. The 8.5 m-long net was made of 4.8 mm green-colored woven mesh, with a 15 cm-wide cloth collar around the mouth, PVC cod end bucket and General Oceanics model 2030 flowmeter. The net had a mouth slightly larger than the frame (3.70 m × 1.20 m) so the net could be laced around the outside of the frame and flotation buoys. The ends of six 12 mm polypropylene rope riblines running the length of the net were shackeled to the frame for additional support. A 4-point bridle of 6.4 mm wire was attached to the corners of the neuston trawl (Fig. 2b). Drag forces kept the entire bridle and towing wire (except for the two short segments attached to the bottom of the frame) out of the water. A length of 5 cm polypropylene rope was attached between the upper towing points on the frame, as a bridle for use in deploying and retrieving the net. A line attached to the retrieval bridle was passed to a hydraulic capstan through a block tied in the rigging over the deck. During a tow, this retrieval line was slackened, but remained attached to the vessel, and floated in a broad arc behind the net mouth.

At each station, the neuston trawl and Manta net were towed simultaneously from the port and starboard outriggers, at approximately 1–1.5 m/second. Tows were generally made either against or with the direction of the prevailing swells. The Manta net was usually fished for approximately 8–9 minutes/tow and filtered about 300–400 m^3. The neuston trawl generally filtered 2,000–3,000 m^3 during a 10–11 minute tow. Additional tows with the neuston trawl were frequently made at a station to assess small-scale patchiness and to sample visible "structures" in the surface layer, such as convergence zones marked by foam lines and rafts of the pleustonic hydroid *Velella velella*.

On several cruises, onset of high winds and rough sea conditions prevented use of the Manta net during the daytime sampling of the transect as we returned toward shore. However, we were able to fish the neuston trawl in winds up to an estimated 40–45 km/hour, and in white-capped seas of 2–3 m. Neuston trawl samples were collected at alternate stations during the periods of adverse weather.

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

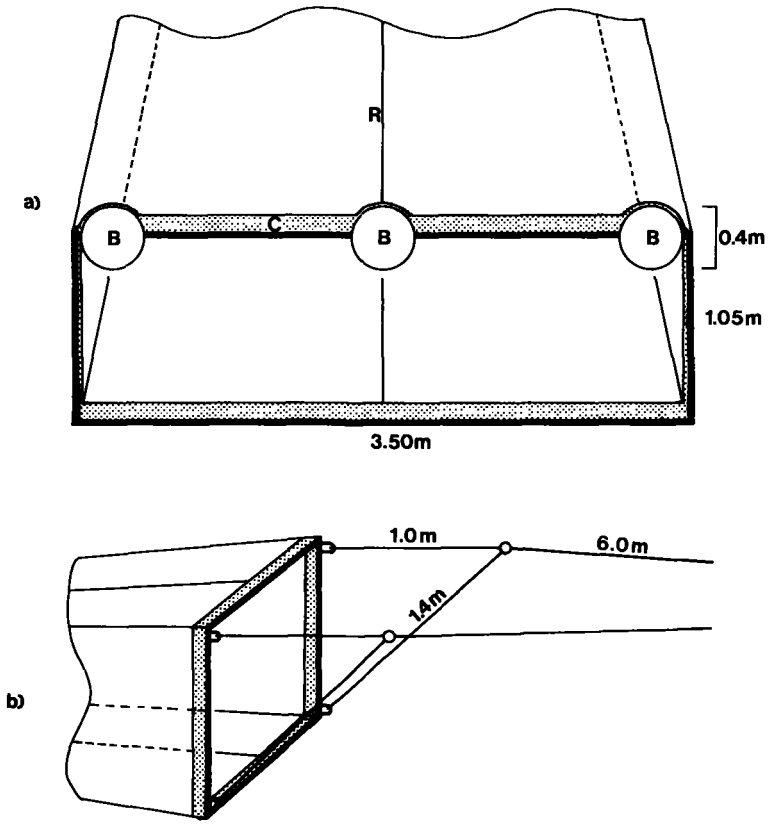

FIGURE 2a.—Front view of the neuston trawl; B = inflated 40 cm diameter spar buoys; C = cloth collar around mouth of net; R = polypropylene rib lines.
FIGURE 2b.—Side view of the neuston trawl showing construction of the towing bridle. Floats were removed for clarity.

Several very large catches of Dungeness crab megalopae in the neuston trawl were subsampled by volume, with the majority of the megalopae being returned alive to the ocean. Samples from both nets were preserved in 10% formalin/seawater and sent to the laboratory for analysis. All larval and juvenile fishes were identified to the lowest practical taxonomic level. After extrapolating catch sizes from subsample counts, the data were normalized to produce density estimates of organisms/1,000 m^3. As an indicator of patchiness of abundant taxa, the coefficient of dispersion (C.D. = $S^2/\overline{X}$) was calculated for the samples in which each taxon was present.

Hydrographic and meteorological data were collected at each station. Surface water temperature was determined with a handheld bucket thermometer. Water samples were collected for laboratory analysis of surface salinity using a Model 8400 Guildline Autosalinometer. A 200 mL surface water sample was filtered through a 0.3 μm pore size Gelman A/E glass fiber filter for determination of chlorophyll a concentration. The filters were stored in dessicant over dry ice at sea, and then in a freezer, before acetone extraction of the chlorophyll a and analysis with a Turner Designs Model 10 Fluorometer. During the daytime, Secchi depths were estimated, using a 30 cm disc, and surface irradiance was measured with a handheld General Electric Model 214 Light Meter. Other data collected included weather and sea state conditions at each station.

RESULTS

Hydrographic Data

The neustonic realm was characterized by distinct temporal and spatial patterns that reflect the highly dynamic springtime oceanographic

processes of the Oregon coastal zone. Daily upwelling indices derived from barometric pressure data (Fig. 3; A. Bakun[4]) indicated that in April and May, local winds varied in direction and strength, with one extended period of stormy weather with southwest winds (negative index values). Temperature and salinity profiles during these months showed relatively little variation along the transect within a sampling period (Fig. 4a, b, c). Chlorophyll a peaks and low salinity near shore may have been due to the influence of water exiting Yaquina Bay. The highest chlorophyll a values were observed following periods of northwest winds, and the highest temperatures occurred after a period of very light winds and high insolation.

The hydrographic regime was altered by the onset of northwest winds in June (Fig. 3), which induced the upwelling of cold, more saline nutrient-rich water along the coast. Strong upwelling [defined by Small and Menzies (1981) as a daily index value >50] was sporadic in June but nearly continuous in July. Temperature, salinity, and chlorophyll a profiles rapidly changed in response to the upwelling-favorable winds (Fig. 5a, b, c).

During the 8–10 June cruise, low temperature and high salinity water was found within 5 km of the coast. Low salinity, warm water more than 15 km offshore apparently was the plume of the Columbia River. By 19–20 June, continued offshore transport of the surface layer pushed the inshore edge of the plume to 40 km off the coast. Low chlorophyll a concentrations, low temperatures, and high salinity near shore on 19–20 June indicated the occurrence of active upwelling.

Upwelling persisted through the end of July. Temperature and salinity profiles were similar to those observed during the second June cruise, with the patterns of increasing temperature and decreasing salinity farther offshore continuing to the limits of sampling of 90 km on 8 and 9 July and to 70 km on 23 and 24 July. During the upwelling in July, a dramatic phytoplankton bloom occurred in the surface waters within 30 km of the coast. Chlorophyll a concentrations here were denser and broader in offshore extent than the surface and subsurface biomass concentrations previously observed off Oregon (Small and Menzies, 1981).

[4]A. Bakun, Pacific Environmental Group, National Marine Fisheries Service, Monterey, CA 93940, pers. commun. August 1984.

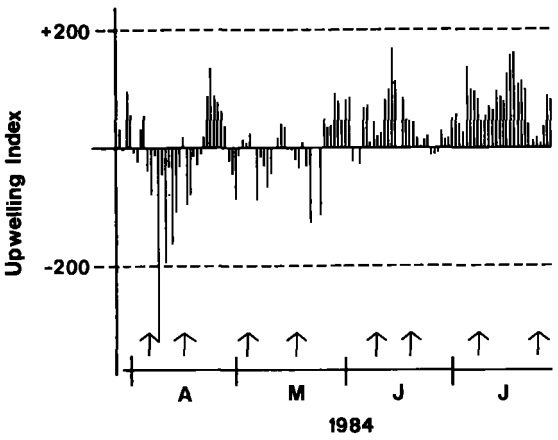

FIGURE 3.—Daily upwelling indices for spring-summer 1984. Positive values >50 indicate occurrence of winds inducing strong upwelling. Arrows indicate dates of sampling cruises.

Ichthyoneuston

A total of 107 Manta net and 142 neuston trawl samples collected 48 taxa of larval, juvenile, and adult fishes. Larvae ≤10 mm and a few juveniles were collected by the Manta net, while large numbers of juvenile fishes up to 60–70 mm were taken by the neuston trawl. Size-frequency data for three of the commonest species (Fig. 6 a, b, c) illustrate the relative ability of the nets to capture different sizes of fishes.

Nighttime sampling (59% of the Manta net tows and 62% of the neuston trawl tows) accounted for 93.3% of all fishes in the Manta net catch and 96.5% of the fishes taken in the neuston trawl (Table 1). Four Manta net and 8 neuston trawl tows made during twilight collected 5.4% and 2.9%, respectively, of the total number of fishes taken with each gear type (Table 2). Only 1.3% of the Manta net catch and 0.6% of the neuston trawl catch was made during daytime (Table 2).

Only two species were not collected predominantly at night. Larval Pacific saury, *Cololabis saira*, were taken in both day and night Manta net samples. Larval northern lampfish, *Stenobrachius leucopsarus*, were abundant only in the twilight samples from early June (Tables 1, 2).

Arbitrary criteria on frequency of occurrence (in >15% of the night samples of either net) or abundance (peak densities >40/1,000 m^3) indicated that nine taxa of larval, juvenile, and adult fishes were dominant components of the ichthyoneuston. Most taxa were characterized by dis-

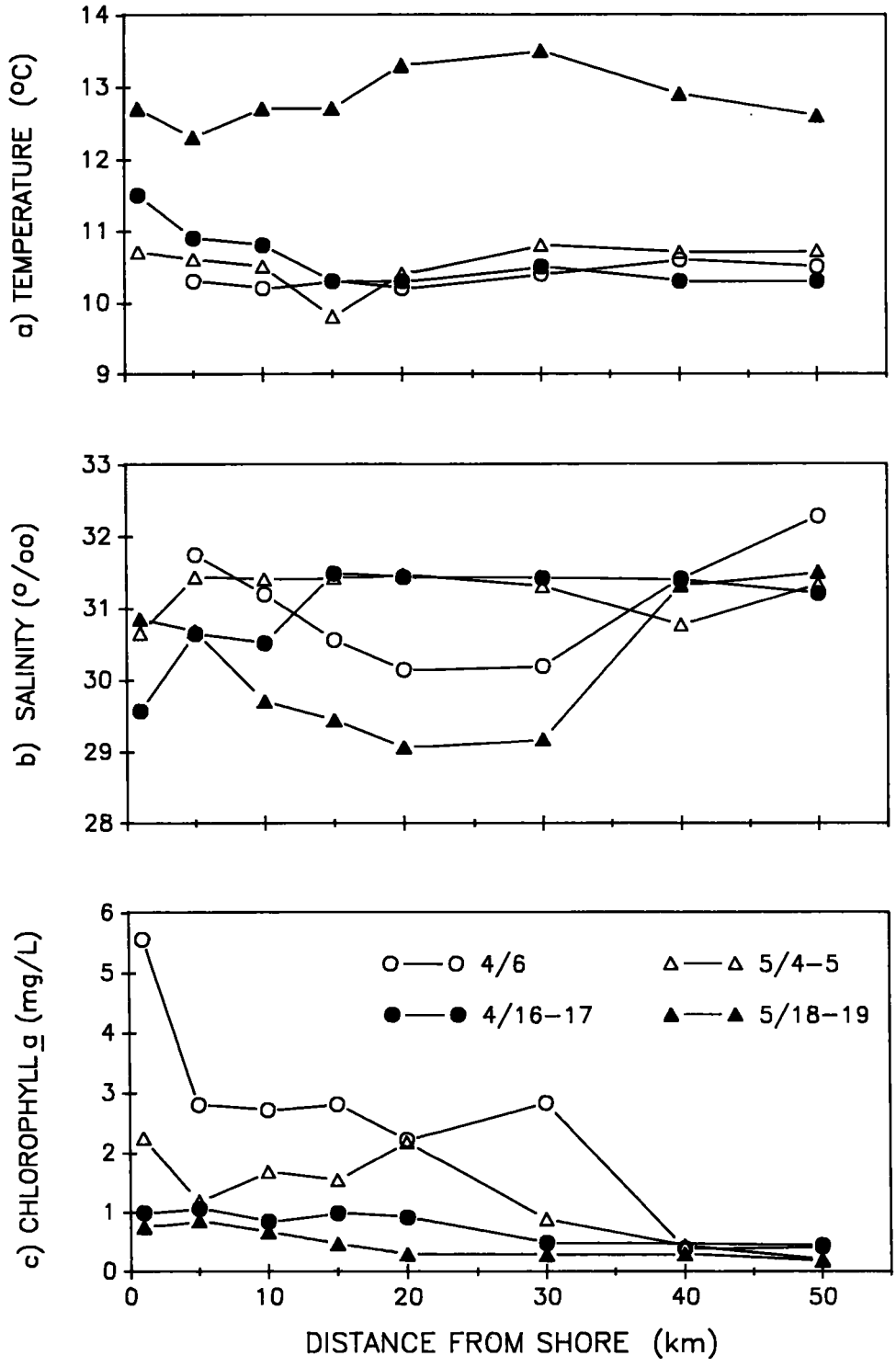

FIGURE 4a-c.—Nighttime environmental conditions observed on each cruise during the pre-upwelling period. a = temperature; b = salinity; c = chlorophyll *a* concentration.

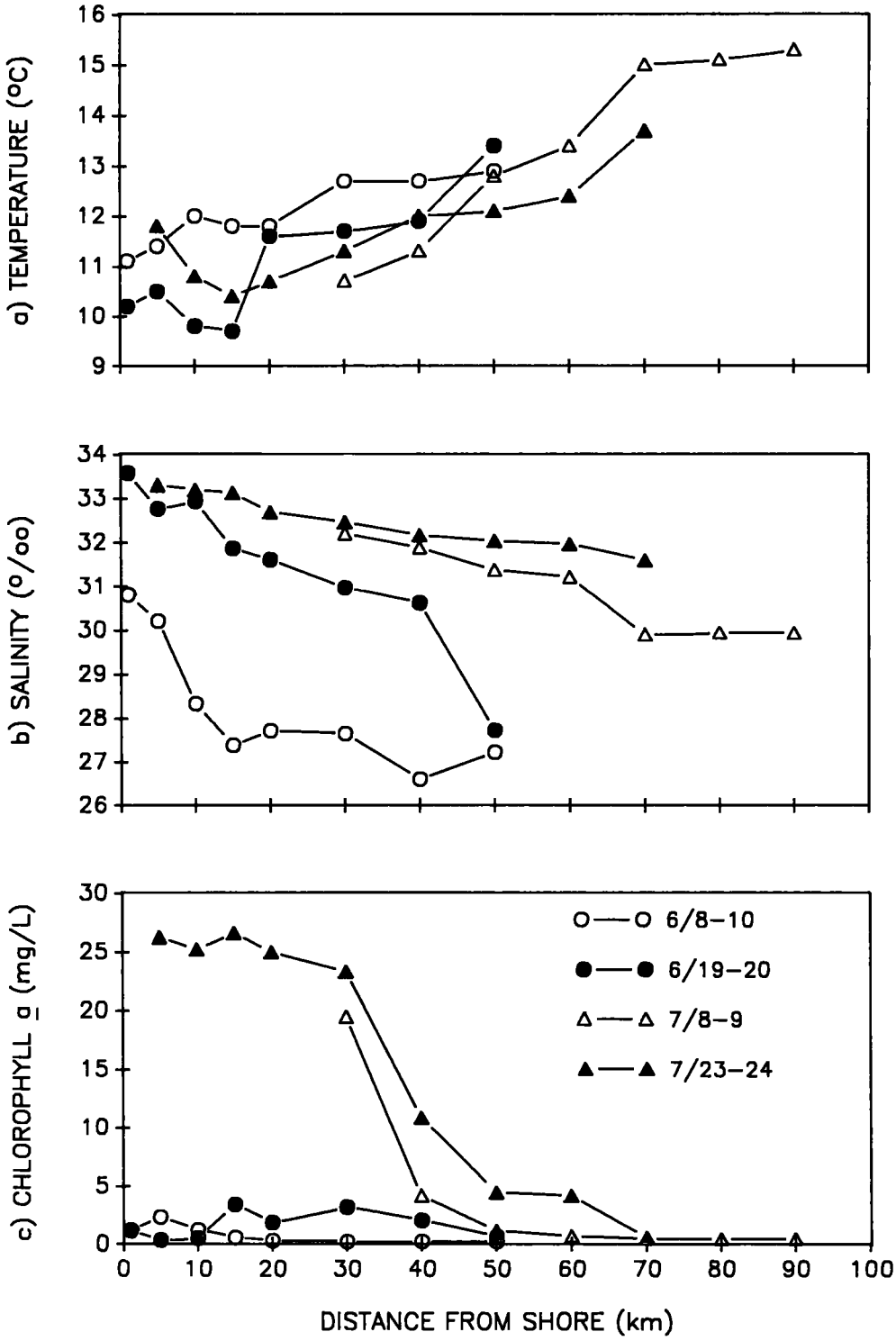

FIGURE 5a-c.—Nighttime environmental conditions observed on each cruise during the upwelling period. a = temperature; b = salinity; c = chlorophyll *a* concentration.

tinct temporal shifts in occurrence: Five taxa were abundant only prior to the onset of continuous upwelling in mid-June, three taxa were sporadically abundant following the beginning of upwelling, and one species (*Ronquilus jordani*) was present throughout the survey.

Pre-upwelling Species

The numerically dominant species in the nearshore region in spring was larval English sole, *Parophyrys vetulus*. These larvae were patchily distributed (C.D. = 32.5) within 30 km offshore, reaching densities of 75/1,000 m^3 in Manta net collections. Larval abundance declined rapidly after April (Table 1). Size-frequency distributions indicated that the Manta net was more effective than the neuston trawl for collecting fish ≤15 mm (Kolmogorov-Smirnov test, $P < 0.01$). Eye migration in the larger fish (20–24 mm) was nearly complete, indicative of their impending shift to a benthic existence. Similar-sized juveniles were taken nearshore in April in benthic tows (B. Mundy[5]).

Cabezon, *Scorpaenichthys marmoratus*, larvae were most abundant in Manta catches in the spring (Table 1), although newly hatched larvae were collected near shore through June. The smallest larvae (4–6 mm) were taken only at the 1–15 km stations, while larvae up to 10 mm were found along the entire transect. These larvae were patchily distributed, with April densities reaching 207/1,000 m^3 (C.D. = 92.7). Frequency of occurrence and larval density declined through early July. Large juvenile cabezon (26–38 mm) were collected by the neuston trawl (Fig. 6a). These juveniles were encountered all along the transect from April to mid-June.

Two dominant taxa found at all stations prior to upwelling were greenling (*Hexagrammos* sp.) and brown Irish lord, *Hemilepidotus spinosus*. Juvenile greenlings were the most frequently collected species, occurring in 44.8% of the nighttime neuston trawl samples (Table 1), although they were rarely taken by the Manta net (Fig. 6b). They were the most evenly dispersed of the abundant fish collected (C.D. = 2.2), and never exceeded densities of 10/1,000 m^3. The two largest catches of greenling were made in association with distinct hydrographic features. Nineteen juveniles were collected from a convergence zone near shore in mid-May (along with 150,000 Dungeness crab megalopae) and 20 juveniles were taken from Columbia River plume water 50 km offshore in early June. Mean lengths of greenling from the neuston trawl samples increased from

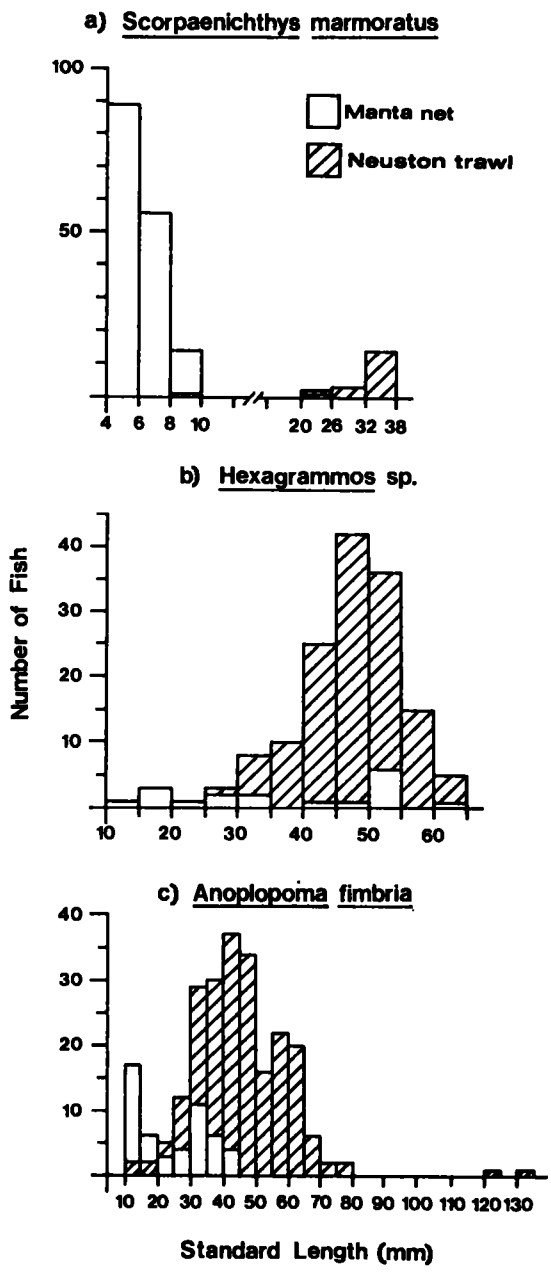

FIGURE 6a-c.—Length-frequency data of larval and juvenile fishes collected by each net. a = *Scorpaenichthys marmoratus*; b = *Hexagrammos* sp.; c = *Anoplopoma fimbria*.

[5]B. C. Mundy, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822, pers. commun. May 1984.

TABLE 1.—Nighttime abundance (A = mean of all catches/1,000 m^3) and frequency of occurrence (F = number of catches) of all ichthyoneuston taxa collected by each net during each month of the survey in 1984.

Species	April				May				June				July				Total			
	Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl	
	A	F(15)	A	F(23)	A	F(16)	A	F(22)	A	F(19)	A	F(24)	A	F(15)	A	F(18)	A	F(65)	A	F(87)
Clupeidae																				
Clupea harengus	3.67	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3.67	2	—	—
Engraulidae																				
Engraulis mordax	—	—	—	—	—	—	—	—	1.98	1	0.25	1	127.90	5	0.28	1	106.91	6	0.27	2
Salmonidae																				
Oncorhynchus keta	—	—	—	—	—	—	0.51	1	—	—	—	—	—	—	—	—	—	—	0.51	1
O. kisutch	—	—	—	—	—	—	0.73	2	—	—	—	—	—	—	0.41	3	—	—	0.54	5
Salmo gairdneri	2.59	1	—	—	—	—	0.60	2	—	—	—	—	—	—	—	—	2.59	1	0.60	2
Osmeridae																				
unidentified	8.78	2	0.40	1	—	—	0.37	1	—	—	—	—	4.32	2	—	—	6.55	4	0.39	2
Sternoptychidae																				
Danaphos oculata	—	—	—	—	—	—	—	—	—	—	—	—	1.68	1	—	—	1.68	1	—	—
Myctophidae																				
Diaphus theta	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.71	1	—	—	0.71	1
Stenobrachius leucopsarus	—	—	0.43	1	2.36	1	—	—	2.16	1	—	—	2.82	2	—	—	2.54	4	0.43	1
Symbolophorus californianus	—	—	—	—	—	—	—	—	—	—	—	—	1.81	1	0.52	3	1.81	1	0.52	3
Tarletonbeania crenularis	—	—	—	—	—	—	0.43	1	6.28	1	0.38	1	153.11	5	42.71	5	128.64	6	30.62	7
Gadidae																				
Microgadus proximus	—	—	—	—	—	—	—	—	—	—	1.02	1	—	—	0.42	1	—	—	0.72	2
Scomberesocidae																				
Cololabis saira	2.76	3	0.36	2	—	—	0.43	1	7.27	3	0.34	4	2.33	5	1.30	3	3.79	11	0.64	10
Gasterosteidae																				
Gasterosteus aculeatus	—	—	—	—	—	—	0.32	1	—	—	—	—	—	—	1.29	1	—	—	0.81	2
Bathymasteridae																				
Ronquilus jordani	4.50	5	—	—	5.59	6	—	—	4.53	11	—	—	15.54	5	0.33	2	6.80	27	0.33	2
Cryptacanthodidae																				
Delolepis gigantea	2.63	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.63	1	—	—
Lyconectes aleutensis	5.00	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5.00	1	—	—
Ammodytidae																				
Ammodytes hexapterus	2.58	4	—	—	9.71	1	—	—	1.64	1	—	—	—	—	—	—	3.61	6	—	—
Stromateidae																				
Icichthys lockingtoni	—	—	—	—	—	—	—	—	—	—	—	—	5.36	3	—	—	5.36	3	—	—
Scorpaenidae																				
Sebastes crameri	—	—	0.44	1	—	—	0.75	3	2.65	2	0.94	9	—	—	—	—	2.65	2	0.86	13
S. melanops	—	—	—	—	—	—	—	—	—	—	0.42	3	—	—	1.01	1	—	—	0.57	4
S. pinniger	—	—	—	—	—	—	0.38	1	—	—	0.28	1	—	—	0.53	2	—	—	0.43	4
S. reedi	—	—	—	—	—	—	—	—	1.74	3	—	—	—	—	0.34	1	1.74	3	0.34	1
Sebastes spp. larvae	19.42	4	—	—	10.42	4	—	—	18.58	8	—	—	238.28	6	—	—	77.07	22	—	—
Sebastes spp. juveniles	—	—	0.43	2	8.99	4	1.62	6	—	—	0.49	7	1.42	2	—	—	6.47	6	0.93	15
Anoplopomatidae																				
Anoplopoma fimbria	3.09	4	1.35	4	10.35	6	3.18	3	8.68	5	11.73	7	—	—	0.34	2	7.86	15	5.97	16
Hexagrammidae																				
Hexagrammos sp.	3.85	4	0.79	13	3.60	5	1.31	11	1.83	4	1.80	15	—	—	—	—	3.07	13	1.33	39
Ophiodon elongatus	12.91	2	—	—	6.28	2	—	—	—	—	—	—	—	—	—	—	9.59	4	—	—
Oxylebius pictus	—	—	0.61	1	—	—	—	—	1.64	1	0.52	1	1.61	1	0.30	1	1.63	2	0.48	3

TABLE 1.—*Continued*.

Species	April				May				June				July				Total			
	Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl	
	A	F(15)	A	F(23)	A	F(16)	A	F(22)	A	F(19)	A	F(24)	A	F(15)	A	F(18)	A	F(65)	A	F(87)
Cottidae																				
Artedius harringtoni	3.44	3	—	—	9.71	1	0.36	1	4.51	3	—	—	1.74	1	—	—	4.39	8	0.36	1
Cottus asper	15.68	2	—	—	—	—	—	—	4.47	2	—	—	—	—	—	—	10.07	4	—	—
Hemilepidotus spinosus	5.45	3	1.05	12	7.39	7	6.11	15	2.40	3	3.77	6	—	—	—	—	5.79	13	3.84	33
Leptocottus armatus	19.09	1	—	—	2.22	1	—	—	—	—	—	—	—	—	—	—	10.66	2	—	—
Scorpaenichthys marmoratus	47.19	10	0.47	5	15.16	5	0.37	3	3.11	10	0.76	5	2.66	2	—	—	21.63	27	0.56	13
Agonidae																				
Agonopsis vulsa	—	—	0.37	1	—	—	0.45	2	—	—	0.46	4	—	—	0.34	2	—	—	0.42	9
Liparididae																				
unidentified	3.99	2	1.28	1	—	—	—	—	2.91	6	0.57	7	3.85	4	0.34	3	3.39	12	0.57	11
Bothidae																				
Citharichthys sordidus	—	—	0.41	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.41	1
C. stigmaeus	—	—	0.43	4	—	—	0.67	2	1.98	1	1.24	7	—	—	0.50	4	1.98	1	0.81	17
Pleuronectidae																				
Eopsetta jordani	—	—	—	—	—	—	0.39	2	—	—	0.71	2	—	—	—	—	—	—	0.55	4
Glyptocephalus zachirus	2.50	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.50	1	—	—
Isopsetta isolepis	—	—	0.41	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.41	1
Parophrys vetulus	22.38	6	4.42	9	2.53	3	0.68	5	1.59	1	0.25	1	—	—	—	—	14.35	10	2.89	15
Pleuronichthys sp.	—	—	—	—	—	—	—	—	—	—	0.51	1	—	—	—	—	—	—	0.51	1
Psettichthys melanostictus	9.48	3	—	—	—	—	—	—	8.04	1	6.61	2	2.20	1	—	—	7.74	5	6.61	2
Unidentifiable	7.92	4	—	—	—	—	0.51	1	2.32	3	—	—	3.89	3	—	—	5.29	10	0.51	1
Total number of taxa	22		16		13		20		21		20		17		17		33		34	
Mean abundance/1,000 m^3	63.53		3.39		22.68		6.43		20.64		7.48		199.91		12.81		72.49		7.24	

TABLE 2.—Daytime abundance (A = mean of all catches/1,000 m^3) and frequency of occurrence (F = number of samples) of all ichthyoneuston taxa collected by each net during the first 3 months of the survey. Daytime samples were not collected in July. Twilight sampling (45 minutes before and after sunset and sunrise) was conducted at the 50 km station on 8-10 June, 1984.

	April				May				June				Daytime total				June twilight			
	Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl		Manta		Trawl	
Species	A	F(15)	A	F(17)	A	F(8)	A	F(12)	A	F(13)	A	F(18)	A	F(36)	A	F(47)	A	F(6)	A	F(8)
Engraulidae																				
Engraulis mordax	—	—	—	—	—	—	—	—	2.41	4	—	—	2.41	4	—	—	—	—	—	—
Osmeridae																				
unidentified	—	—	—	—	—	—	—	—	1.56	1	—	—	1.56	1	—	—	—	—	—	—
Myctophidae																				
Stenobrachius leucopsarus	—	—	—	—	—	—	—	—	1.89	1	—	—	1.89	1	—	—	27.62	3	—	—
Scomberesocidae																				
Cololabis saira	2.48	4	—	—	—	—	—	—	2.44	4	—	—	2.46	8	—	—	2.75	3	—	—
Bathymasteridae																				
Ronquilus jordani	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.71	3	—	—
Cryptacanthodidae																				
Lyconectes aleutensis	2.54	1	—	—	—	—	—	—	—	—	—	—	2.54	1	—	—	—	—	—	—
Ammodytidae																				
Ammodytes hexapterus	—	—	—	—	—	—	—	—	—	—	0.33	1	—	—	0.33	1	—	—	—	—
Scorpaenidae																				
Sebastes crameri	—	—	—	—	—	—	0.32	1	—	—	—	—	—	—	0.32	1	—	—	0.97	2
S. mystinus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.50	1	—	—
Sebastes spp. larvae	—	—	—	—	—	—	—	—	5.39	2	—	—	5.39	2	—	—	4.59	2	—	—
Sebastes spp. juveniles	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4.50	1	0.50	2
Anoplopomatidae																				
Anoplopoma fimbria	2.60	1	—	—	2.87	1	0.38	1	—	—	—	—	2.74	2	0.38	1	2.30	2	1.48	5
Hexagrammidae																				
Hexagrammos sp.	2.74	2	0.81	2	—	—	—	—	—	—	—	—	2.74	2	0.81	2	—	—	1.10	3
Ophiodon elongatus	2.52	2	—	—	—	—	—	—	—	—	—	—	2.52	2	—	—	—	—	—	—
Cottidae																				
unidentified	—	—	—	—	1.57	2	—	—	—	—	—	—	1.57	2	—	—	—	—	—	—
Clinocottus globiceps	—	—	—	—	—	—	—	—	1.57	1	—	—	1.57	1	—	—	—	—	—	—
Hemilepidotus spinosus	—	—	—	—	—	—	0.35	1	—	—	—	—	—	—	0.35	1	10.30	2	1.17	7
Scorpaenichthys marmoratus	2.52	2	—	—	—	—	—	—	1.58	1	—	—	2.20	3	—	—	1.93	1	0.46	1
Liparididae																				
unidentified	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.37	1
Pleuronectidae																				
Eopsetta jordani	—	—	—	—	—	—	—	—	1.61	1	—	—	1.61	1	—	—	—	—	—	—
Parophrys vetulus	2.76	1	0.94	1	—	—	0.32	1	—	—	—	—	2.76	1	0.63	2	—	—	—	—
Unidentifiable	—	—	—	—	—	—	—	—	1.89	2	—	—	1.89	2	—	—	—	—	—	—
Total number of taxa	7		2		2		4		9		1		15		6		9		7	
Mean abundance/1,000 m^3	2.22		0.15		0.75		0.11		3.24		0.02		2.26		0.08		24.60		2.83	

38.8 mm ($N = 10$) in early April to 51.2 mm ($N = 72$) during the first June cruise.

Brown Irish lord juveniles were the numerically most abundant and the second most frequently occurring species (Table 1). Early juveniles (10–20 mm) were taken with both nets in April and May only at the offshore (40–50 km) stations. Larger juveniles (20–30 mm) were patchily distributed from April through mid-June all along the transect (C.D. = 14.1). Although 47% of the total number of trawl caught specimens were taken in densities below 15/1,000 m^3, repeated sampling in one large aggregation accounted for the bulk of the catch. Three sequential tows at the 50 km station on 5 May had juvenile densities of 15–39/1,000 m^3 , but distinctive hydrographic characteristics at the station were not detected.

The only species with a characteristic offshore distribution prior to upwelling was sablefish, *Anoplopoma fimbria*. Small juveniles (10–45 mm) were effectively taken by the Manta net, while the neuston trawl was more efficient at collecting 30–70 mm specimens (Fig. 6c). The 10–50 mm fish were collected primarily at the 50 km station from April through mid-June, although several specimens were taken closer inshore. The 50–75 mm fish were captured only on 8–10 June from the Columbia River plume water at the 50 km station. After the onset of upwelling, two individuals (120–130 mm) were taken 80–90 km from shore.

Upwelling Species

Three taxa were abundant on only one of three cruises made after the onset of upwelling in mid-June (Table 1). Distributions of northern anchovy, *Engraulis mordax*, larvae; rockfish (*Sebastes* spp.) larvae; and adult blue lanternfish, *Tarletonbeania crenularis*, overlapped at some offshore stations on 8 and 9 July. The offshore portion of the transect was characterized by a drop in salinity and an increase in temperature between 60 and 70 km offshore (Fig. 5a, b), indicating a transition from coastal to Columbia River plume water.

Of the 814 rockfish larvae collected throughout the survey, 87% were taken at the 50–90 km stations on this cruise, with a peak density of the 3.5–7.0 mm larvae of 684/1,000 m^3. Adult blue lanternfish were present in densities up to 315/1,000 m^3 at the 60–90 km stations. Lanternfish from simultaneous Manta and neuston trawl tows displayed no difference in length-frequency distributions, although a significant change in the size structure of the catches between stations was observed (K-S test, $P < 0.01$). Mean size of the fish decreased approximately 10% between adjacent stations, from 50.9 mm at 60 km to 37.8 mm at 90 km. Anchovy larvae (3–9 mm) were restricted to the lower salinity plume water at the 70–90 km stations, with peak and mean densities of 368 and 210/1,000 m^3, respectively.

Persistant Species

Only northern ronquils, *Ronquilus jordani*, were abundant in both pre-upwelling and upwelling periods. The elongate larvae and juveniles were collected with the Manta net starting in mid-April, with abundances peaking at 40/1,000 m^3 in July. Mean lengths over this time interval increased from 8.7 mm ($n = 8$) to 26.6 mm ($n = 43$). Ronquils were relatively dispersed along the transect (C.D. = 7.6), and size or seasonal patterns of distribution were not detected.

Dungeness Crab Megalopae

Dungeness crab megalopae were the dominant component of the catches throughout the survey, with an estimated total of 350,000 megalopae collected in 249 hauls. The megalopae were found at most stations during all cruises (Fig. 7), although they were rare seaward of 50 km in July. Megalopae were present in 71.4% of the Manta net daytime tows and 93.8% of the nighttime tows, and in 90.9% and 98.9% of the day and night neuston trawl collections, respectively. All twilight hauls captured megalopae.

Despite the higher frequency of occurrence of megalopae in the neuston trawl, the Manta net was a more accurate estimator of their abundance. For 58 pairs of nighttime catches with densities under 2,000/1,000 m^3, the Manta net caught approximately 3 times as many megalopae per m^3 as the neuston trawl. The 4.8 mm mesh of the neuston trawl apparently enabled some megalopae to pass through the mesh, and some escapement was observed while the trawl was sitting on deck after retrieval. More similar estimates between the nets were obtained when higher densities of megalopae were sampled, probably because of clumping of the large (11 mm total length) spiny megalopae into large masses which clogged the mesh.

In general, densities of megalopae caught by

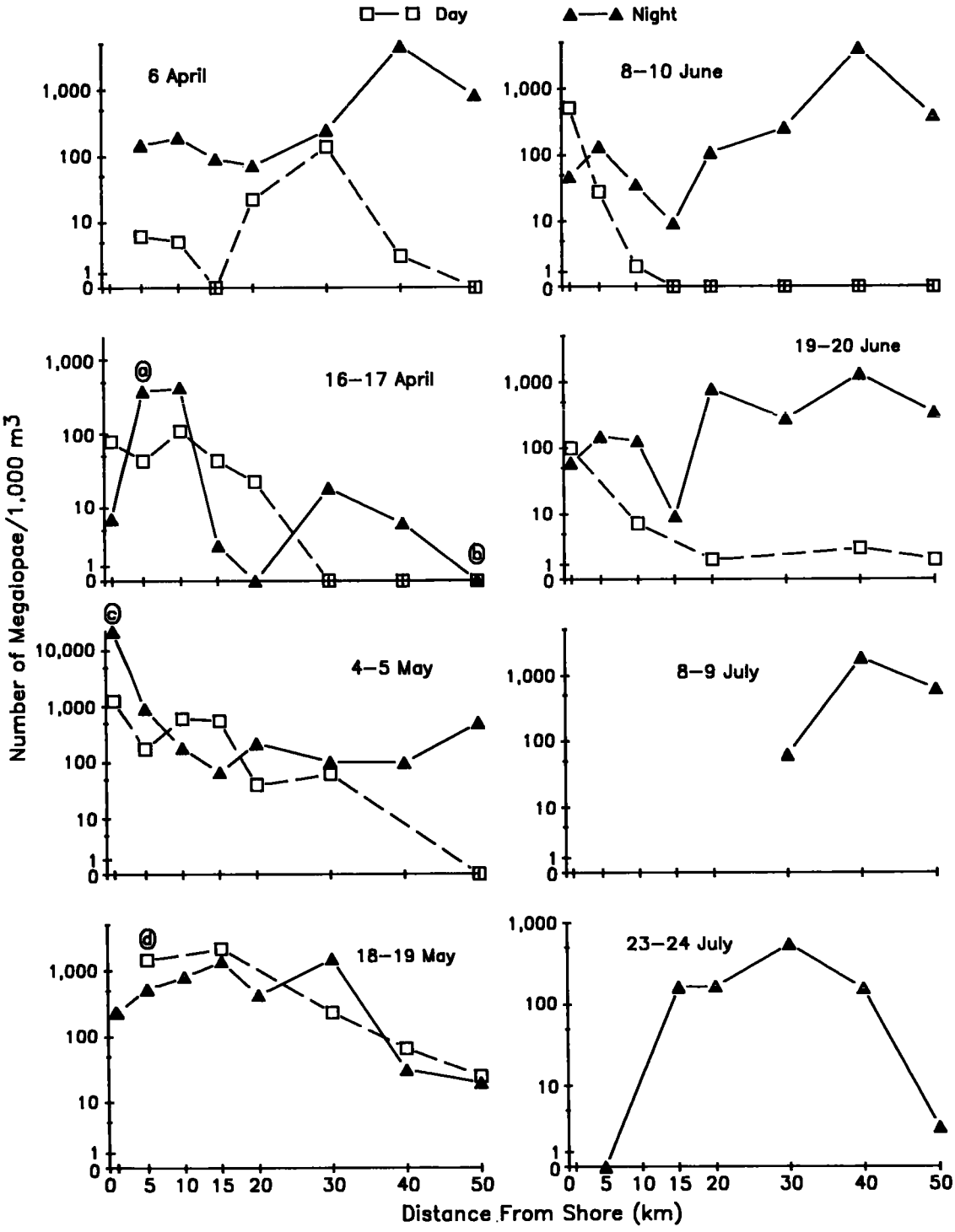

FIGURE 7.—Daytime and nighttime densities of megalopae collected by the Manta net. Rough weather prevented the use of the Manta net during the day of 19 May; neuston trawl data for this portion of the cruise are presented. Circled letters refer to events discussed in the text.

the Manta net in the daytime were lower than at night for each station (Fig. 7). The differences between day and night were particularly apparent on bright sunny days and at the offshore stations. Only one of 13 samples of megalopae collected when light intensity exceeded 4,000 lux had a density over 200/1,000 m^3, while 12 of 24 day samples collected at lower light levels exceeded this density. Highest daytime densities (1,600–2,400/1,000 m^3 in neuston trawl samples) were observed on 19 May when a sudden shift in weather before daybreak resulted in very dark, overcast and rainy skies, with 40–45 km/hour winds and 2–3 m breaking waves.

Water clarity may also affect the daytime abundance estimates of megalopae in the neuston along the transect. Daytime densities were always low seaward of 30 km where Secchi depths exceeded 9 m, while higher densities were observed in the more turbid near-coastal waters with Secchi depths of 4–9 m.

The 27-h occupancy of the 50 km station on 8–9 June provided additional evidence of a distinct diel pattern in utilization of the neustonic habitat by megalopae (Fig. 8). Abundance of megalopae peaked during the twilight periods of dawn and dusk. A significant decrease in abundance was noted in the middle of the night, while midday samples did not collect any megalopae.

In addition to the wide distribution of megalopae along the transect, sampling occasionally detected the aggregation of very large numbers of megalopae (denoted by letters over station blocks in Figure 7). These aggregations were typically associated with hydrodynamic or biological structures in the surface layer.

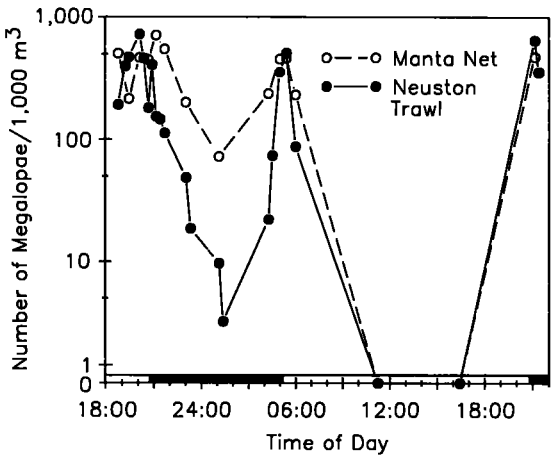

FIGURE 8.—Density of megalopae collected by both nets during a 27 h sampling period 50 km offshore on 8–9 June.

Event A: Simultaneous tows with the Manta net and neuston trawl caught megalopae in densities of 373 and 325/1,000 m^3. The neuston trawl was then redeployed and towed along a foam line marking a surface convergence. An estimated 60,000 megalopae were collected from the convergence zone (24,000/1,000 m^3).

Event B: A series of five consecutive tows with the trawl net was made. Each tow covered a linear distance of approximately 1 km in a westward direction, with an estimated distance of 300 m between tows. Megalopae were very sparse in the simultaneous Manta and trawl tows at the beginning of the series, with densities of 0 and 1.9/1,000 m^3, respectively. The subsequent neuston trawl tows produced density estimates of 79, 3,555, 2,414 and 187/1,000 m^3. Apparently, the megalopae were aggregated over an area extending at least 5 km in the east-west direction.

Event C: Following a period of southwest winds, a large raft of *Velella velella* was found around the inshore station. *Velella velella* were generally found at offshore stations but at densities far lower than the 36 kg/1,000 m^2 level taken here. Although the overall extent of the raft could not be determined at night, the density of megalopae was estimated by both nets at 21,500/1,000 m^3.

Event D: The density of megalopae sampled by the Manta net was 790/1,000 m^3, while a simultaneous neuston trawl tow along a convergence zone only 30 m away collected 150,000 megalopae (46,400/1,000 m^3).

Census estimates of megalopal abundance were computed from nighttime samples for each date (Fig. 9). A modification of Smith's regional census estimate (1972) was used to compute the total number of megalopae occurring in a 1 m wide × 1 m deep track along the surface from the coast to 55 km offshore:

$$C_k = \sum_{i=1}^{n} (A_i D_i)$$

where C_k = estimate of abundance of megalopae per meter of coastline during cruise k

A_i = volume of water in the track surrounding station i, computed from

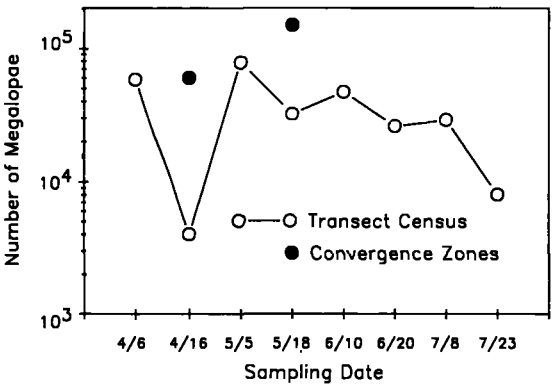

FIGURE 9.—Census estimates of Dungeness crab megalopae at night from Manta net samples for each cruise in a 1 m wide × 1 m deep track extending from the coast to 55 km offshore (30–95 km offshore on 7/8). Single samples from convergence zones sampled with the neuston trawl contained more megalopae than the entire census estimates for the respective cruises.

the midpoints of the distances between the adjacent stations
D_i = density of megalopae at station i.

Although census estimates varied between cruises from approximately 4,000–78,000, these estimates ignored the concentrations of megalopae in convergence zones or other aggregations that were sampled by the neuston trawl. The convergences alone contained 5–15 times more megalopae than the entire census estimates for their respective cruises.

DISCUSSION

The neustonic habitat off Oregon is a dynamic environment that supports an abundant and diverse fauna including Dungeness crab larvae and numerous fish species. The large mouth size of the neuston trawl and minimal disturbance from the vessel probably contributed to larger catches of surface-dwelling ichthyofauna than have been made in previous studies in the same region (Boehlert et al. 1985).

Several species of neustonic organisms were associated with specific oceanographic features such as convergence zones and water masses like the Columbia River plume. These aggregations of Dungeness crab megalopae and several fish species accounted for the major portion of the total catch of each taxon. Recent studies by Shanks (1983, 1985) and Kingsford and Choat (1985, 1986) further emphasize the importance of aggregation of neustonic organisms in oceanic convergences, surface slicks, and around floating objects. This information clearly demonstrates that randomized or grid sampling plans will often fail to detect micro- or meso-scale features of the environment. Surveys may thus severely underestimate the abundance of species, and important data on ecological characteristics such as predator-prey interactions may not be obtained. This is particularly important in understanding the role of spatial co-occurrence of patches of larval fishes and their prey on larval survival and growth (Lasker 1975, 1981; Grover and Olla 1986).

Diel patterns in abundance were striking. Most of the neustonic organisms were collected at night, and their absence from daytime collections may be attributed to vertical migration out of the surface layer or to visual avoidance of the nets. The fact that very few larval or juvenile sablefish and greenlings were collected in subsurface samples in earlier studies (e.g., Richardson and Pearcy 1977; Richardson et al. 1980; Kendall and Clark 1982a; Clark 1984), suggests that these fishes are obligate inhabitants of the neuston, and their low abundance in daytime hauls indicates substantial visual avoidance of the nets.

Conversely, other species may be facultative neuston that undergo diel migrations into the surface layer (Hempel and Weikert 1972), where they can most easily be assessed. Dungeness crab megalopae, in particular, disperse to at least 50 m during the day, but concentrate at the surface at dawn and dusk (Booth et al. 1985). Still other species (the pseudoneuston) may have depth ranges that overlap with the surface layer.

Previous studies on northwest ichthyoplankton have defined basic coastal, transitional, and offshore assemblages of species during different seasons (Richardson and Pearcy 1977; Richardson et al. 1980; Kendall and Clark 1984a, b; Clark 1984). In general, the transitional region roughly parallels the shelf break (approximately 30–40 km offshore in the vicinity of Newport, OR). Richardson et al. (1980) ascribed the consistency of these zonal assemblages to the spawning habits of adults and larval transport in the alongshore coastal circulation. According to Parrish et al. (1981), the spatial and temporal patterns of spawning, and durations of pelagic larval stages of these species, should correspond with the surface drift patterns of the region to minimize larval advection out of suitable habitats. In the Pacific Northwest, species with larvae adapted to the nearshore zone should spawn from fall

through early spring when net surface drift is primarily northward and onshore. Oceanic larvae, however, should be spawned following the spring-summer transition when upwelling results in southward and offshore transport.

The onshore/offshore distributions of several abundant fish species in 1984 were similar to those described earlier, and their seasonal occurrence usually coincided with the constraints discussed by Parrish et al. (1981). However, four species had distributions that crossed the previously described zonal boundaries (Fig. 10). Early cabezon larvae appeared to disperse offshore as they grew. In contrast, early juvenile brown Irish lords were collected offshore in the early spring, while the larger juveniles spread inshore across all stations. Larval greenlings have only been collected close to the coast in late fall (Bates 1984), while the juveniles collected in this study were found at all stations prior to upwelling. Juvenile ronquils were also distributed along the transect, during both non-upwelling and upwelling conditions.

The dispersion of organisms across the transition zone may have been accomplished by several mechanisms. Physical transport of the organisms by mesoscale hydrographic events (e.g., eddies, offshore jets, and meanders in the alongshore currents) (Ikeda and Emery 1984; Mooers and Robinson 1984; Abbott and Zion 1985; Davis 1985) undoubtedly play important roles in the onshore/offshore dispersal of planktonic organisms. Transport with these events may be accelerated or hindered by diel vertical migration into water layers with different zonal flow patterns. Additionally, several species (especially greenling and sablefish) are rapid swimmers whose mobility can contribute to their dispersal or aggregation.

The rapid change in the composition of the ichthyoplankton fauna following the onset of upwelling has not been previously observed. Fishes abundant prior to upwelling may respond to the change in the environment in different ways. The disappearance of greenling and brown Irish lord juveniles suggests upwelling triggered settlement of these fishes to the demersal habitat utilized by older juveniles and adults. A possible stimulus for this transition is the breakdown of the thermocline, which has been identified as a

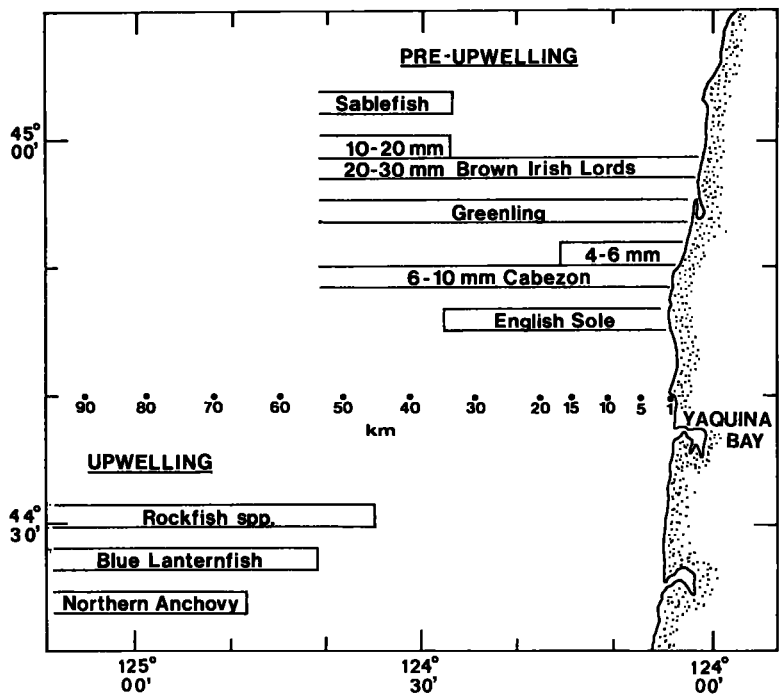

FIGURE 10.—Summary of the zonal distributions of larval and juvenile neustonic fishes in the pre- and early upwelling period (April through mid-June) and the strong upwelling period (July).

barrier to settlement to neustonic juvenile red hake, *Urophycis chuss*, (Steiner et al. 1982; Steiner and Olla 1985).

In contrast, juvenile sablefish apparently remain in the water column off Oregon following the transition to upwelling conditions. Small juveniles (<50 mm) have been captured as far as 250 km offshore in the spring (Kendall and Clark 1982a), and specimens up to 250 mm have been collected from the surface waters in late summer with a purse seine (Brodeur and Pearcy 1986). The very rapid growth rates of young juveniles, reaching 2 mm/day (Boehlert and Yoklavich 1985; Shenker and Olla 1986), undoubtedly resulted in their increasing ability to avoid the towed neuston nets used in this study.

The most abundant larvae occurring after the onset of upwelling were northern anchovy and rockfish. As observed in previous studies (Richardson 1973, 1980; Richardson et al. 1980), these larvae were primarily found offshore. The occurrence of these species, along with a high abundance of vertically migrating blue lanternfish, on the periphery of the Columbia River plume 60–90 km offshore on only one cruise, further illustrates the patchy nature of neustonic distributions.

Although the fish fauna in 1984 was generally characterized by discrete temporal and/or spatial limitations, the occurrence of Dungeness crab megalopae transcended these limits through the 4-mo study. Megalopae were the most abundant organisms collected throughout the survey, but their abundance varied widely between adjacent stations, with occasional very dense patches. Similar patchy distributions of megalopae were observed off British Columbia by Booth et al. (1985), who measured horizontal patch dimensions of 2–4 km. Several dense swarms of megalopae were observed in Bodega Bay, CA, during 1985 (Shenker and Botsford[6]). These patches were long, sinuous aggregations extending 10–20 m along the surface, approximately circular in cross section and about 1 m in diameter. Densities were visually estimated to be on the order of thousands of megalopae per m^3.

The temporal occcurrence of crab larvae in the plankton spans two distinctly different oceanic regimes, and the larvae are potentially transported long distances by the seasonal currents. Larvae typically hatch in mid-winter, pass through 5 zoeal stages in approximately 90 days, and then a month-long megalops stage before settling to the bottom (Reilly 1983a). After hatching, zoeae are released into the northerly flowing Davidson Current. Despite a general onshore component of flow of the Davidson Current, older zoeal stages have been found progressively farther offshore (Lough 1976; Reilly 1983a).

About the time of the spring transition in the alongshore currents from a northerly to southerly direction (Huyer et al. 1975), zoeae metamorphose into megalopae. To survive, these megalopae must be transported back toward the shore, and settle to the bottom in depths shallower than 25 m (Reilly 1983b). Larvae have been found at least 100 km from shore (Lough 1976), although it is unclear if these larvae make it back to shore, or are simply lost from the population.

Again, an apparent anomaly exists between the directions of movement of megalopae and surface waters, where the Ekman layer moves offshore in response to upwelling winds. These discrepancies may be explained by mesoscale mixing processes, as cited earlier. Alternatively, the diel vertical movements of the larvae can move them into different water masses with different directions of zonal movement.

The data from this study and previous research on vertical migration indicate that at least the early zoeal stages and megalopae move to the surface during twilight, and below the surface during the day (Reilly 1983a). Surface abundance estimates of megalopae obtained in the 27-h sampling on 8–9 June (Fig. 8), and by Booth et al. (1985), decreased during the middle of the night. This movement away from the surface is an example of "midnight scattering", perhaps resulting from the lack of a light cue to orient planktonic organisms to the surface (Owen 1981). If midnight scattering is typical for megalopae, abundance estimates made by sampling along a transect throughout the night (Figs. 7, 9) probably underestimate the actual abundance of megalopae utilizing the surface habitat. Megalopae have been collected as deep as 50–70 m during the day (Booth et al. 1985; Shenker and Botsford fn. 6). These observations correlate with Jacoby's (1982) laboratory demonstration that megalopae are positively phototactic to dim light, but avoid bright light.

The present study indicates that the phototactic response of megalopae may assist their return to shore in several ways. Downward movement

[6]Shenker, J. M., and L. W. Botsford, University of California, Bodega Marine Laboratory, P.O. Box 247, Bodega Bay, CA 94923, unpubl. data.

during sunny days, when upwelling wind stress and offshore Ekman transport is generally strongest, can move the larvae into the slow onshore flow below the surface Ekman layer (Peterson et al. 1979). In contrast to the usual northerly upwelling winds, occasional storms blow from the southwest, driving the surface layer onshore. The occurrence of megalopae at the surface during the day was most pronounced on these dark stormy days (especially on the second May cruise), and thus may facilitate their onshore transport.

Observations of megalopae entering into embayments and nearshore areas from Washington to northern California in 1984 and 1985 indicated a dramatic increase in the abundance of megalopae and an extended seasonal occurrence in the plankton, as compared to previous years (Shenker and Botsford fn. 6; Armstrong[7]). This high abundance of crab larvae may presage an upswing in the cyclical crab fishery along these coasts.

Numerous mechanisms have been proposed as causes of the 10-yr cycles in crab abundance. Although some hypotheses have been discounted, several models have survived scrutiny as possible causes of the cycles (see Botsford 1986 for review). Potential mechanisms of environmental forcing of the cycles focus on larval transport and survival. Johnson et al. (1986) detected periodic 10-yr cycles in the occurrence and strength of southward stress during the late larval period that significantly correlated with commercial crab catch 4 and 5 years later. This lag corresponds to the time between larval settlement and growth into the adult fishery (Botsford 1984).

Model simulations by Botsford (1986) indicated that nonlinear effects of wind on larval transport can produce the cyclical swings in crab abundance. However, the models do not preclude the possibility that density-dependent phenomena (such as cannibalism by adult crabs on newly settled juveniles, and predation by nemertean worms on egg masses) may act in concert with the environmental forcing to produce the observed cycles.

The water's surface is the only oceanic habitat that is easily accessible to observation using techniques ranging from satellite and aerial scanning to shipboard visual sighting of targets and continuous monitoring of environmental parameters. Because of this accessibility, micro- and mesoscale patterns in distribution of neustonic taxa and their associations with hydrographic and biological characteristics of the surface zone can be determined more easily than in other environments. The neustonic realm thus offers an excellent opportunity to investigate the mechanisms of transport of the early stages into appropriate nursery habitats, and the availability of food for growth that are required for successful recruitment into adult stocks (Hjort 1914; Lasker 1975, 1981; Frank and Leggett 1982; Sinclair et al. 1984).

[7]D. A. Armstrong, School of Fisheries, WH-10, University of Washington, Seattle, WA 98195, pers. commun. October 1984.

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WINTER-TIME DISTRIBUTION AND ABUNDANCE OF COPEPOD NAUPLII IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Copepod nauplii were collected from continental shelf waters in 3 regions of the northern Gulf of Mexico during winters between 1981 and 1984, off Cape San Blas, Florida, off the Mississippi River delta, and off of Galveston, Texas. Some statistically significant ($P < 0.05$) patterns in the abundance and distribution of nauplii were observed: there was significant interannual variability in naupliar concentrations within the region around the Mississippi River delta; naupliar concentrations in the upper 10 m decreased in the onshore-offshore direction in 2 of 4 comparisons; naupliar concentrations in the upper 10 m differed regionally in 2 of 3 comparisons; and naupliar concentration was correlated with chlorophyll concentration in 4 of 5 comparisons.

Maximum concentrations of nauplii (number per m^3) within a water column were 2–10 times greater at stations influenced by the Mississippi River plumes than in the other 2 regions. This condition in attributed to vertical stratification imparted to the water column by the inflowing low salinity water from the Mississippi River. We conclude that the physical stratification provides a mechanism for the establishment of high concentrations of nauplii that otherwise would not exist in the winter months on the continental shelf.

Microzooplankton are important diet items for larval fish (Arthur 1976; Gamble et al. 1981; Checkley 1982; Govoni et al. 1983; Houde and Lovdal 1984; Stoecker and Govoni 1984), and gut analyses indicate that copepod nauplii are frequently the dominant prey form found in the larvae of many fish species (Duka and Gordina 1973). Available concentrations of microzooplankton are considered an important determinant of larval survival rates in the ocean because this relationship has been demonstrated in the laboratory (Laurence 1974; Houde 1978) and because field studies have demonstrated a relationship between regions or periods of high microplankton and high larval abundance (Arthur 1977; Lasker 1978). Because survival is enhanced by increased food availability, oceanographic processes that result in increased concentration or production of prey items are important.

The gulf menhaden, *Brevoortia patronus* (Clupeiformes), supports the largest volume fishery in the United States (U.S. Department of Commerce 1983). Spawning occurs in the wintertime, from October to March, in continental shelf waters of the northern Gulf of Mexcio (Fore 1970; Lewis and Rothmayr 1981; Warlen 1988), primarily off of Mississippi and Alabama to the east of the Mississippi River delta, and off of Louisiana to the west of the delta. During February and December 1982, concentrations of menhaden larvae in the region near the Mississippi River delta were greater in plume waters than outside and were much higher at the plume front (Govoni and Hoss[3]). Furthermore, gut contents of these larvae indicated that nauplii were the most abundant prey items.

Much of the continental shelf water of the northern and western Gulf of Mexico is vertically unstratified during the winter, and winter is also the season of minimum primary productivity in these regions, as it is in shelf waters of the northeast and southeast United States. However, coastal waters and nearshore regions influenced by freshwater inputs can be physically stratified during winter when low salinity plumes disperse over higher salinity shelf waters. We postulated that shelf waters influenced by fresh water from the Mississippi River plumes would be regions of increased production and concentration of microzooplankton. The purpose of this paper is to examine this hypothesis by describing the vertical and horizontal distribution and abundance of copepod nauplii in shelf waters of the northern Gulf of

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Mexico and by comparing these with oceanographic and hydrographic indicators of water column stratification and productivity.

METHODS

Samples were collected during 5 winter cruises between November and March, during 1981–84, (Table 1). Microplankton samples and hydrographic data were collected from 3 general regions of the northern Gulf of Mexico: off of Galveston, TX, in the region of the Mississippi River delta, and off of Cape San Blas, FL (Fig. 1). Samples were not collected from all 3 regions on each cruise.

Water samples for chlorophyll and nutrient analyses were collected with Niskin bottles. For each chlorophyll analysis, between 25 and 150 mL of seawater was filtered onto a GF/F or GF/C glass fiber filter and homogenized by grinding in 90% aqueous acetone. Fluorescence of the filtrate, brought up to a volume of 10.0 mL, was determined before and after acidification with 2 drops of 10% HCl using a Turner Designs[4] Model 10 fluorometer. Chlorophyll and pheopigment concentrations as chlorophyll equivalents were determined from

$$\text{chlorophyll } (\mu g/L) = \frac{K(f_o - f_a)}{v}$$

$$\text{pheopigment } (\mu g/L) = \frac{K(Rf_a - f_o)}{v}$$

where K is the machine calibration constant, f_o and f_a are the fluorescence readings before and after acidification, R is the acid ratio, and v is the volume of seawater filtered, in mL (Strickland and Parsons 1968).

Samples for nutrient analyses were frozen. Nitrate and nitrite were analyzed according to method number 353.2 described by EPA publication number EPA 600/4-79-020 (Environmental Protection Agency 1979).

Temperature and salinity were measured by several methods. During cruise I, temperature was measured by the temperature sensor on the MOCNESS[5] net, and salinity was measured with a refractometer. During cruises II and III, temperature was measured with expendable bathythermographs (Sippican Instruments). Salinity was measured with a YSI Model 33-S-C-T salinometer on cruise II, and with a Beckman Model RS5-3 salinometer on cruise III. For both of these cruises, bottle samples, analyzed in the laboratory with a Guildline Model 8400A Autosal, were used to check the shipboard salinity measure-

TABLE 1.—Station information, 1981–84.

Station	Date	Time	Depth (m)	Lat. (N)	Long. (W)
I–1	2–13–81	0000	18	29°05′	94°07′
I–2	2–13–81	1200	18	29°06′	94°07′
I–3	2–14–81	0001	90	28°04′	93°03′
I–4	2–14–81	1200	90	28°04′	93°03′
I–5	2–15–81	0000	180	27°54′	92°51′
I–6	2–15–81	1200	180	25°54′	92°50′
I–7	2–16–81	0001	180	28°34′	89°37′
I–8	2–17–81	1200	180	28°35′	89°38′
I–9	2–18–81	0001	90	28°50′	89°16′
I–10	2–18–81	1200	90	28°50′	89°16′
I–11	2–19–81	0000	18	28°56′	89°29′
I–12	2–19–81	1200	18	28°56′	89°29′
I–13	2–20–81	0000	90	29°09′	85°56′
I–14	2–21–81	1200	90	29°08′	85°56′
I–15	2–22–81	0000	180	29°28′	86°07′
I–16	2–22–81	1200	180	29°28′	86°07′
I–17	2–23–81	0001	18	29°36′	85°47′
I–18	2–23–81	1200	18	29°35′	85°47′
I–19	2–24–81	0001	18	30°12′	87°06′
II–1	12–05–82	0700	25	28°53′	89°29′
II–2	12–05–82	1255	62	28°53′	89°32′
II–3	12–05–82	1945	33	28°59′	89°34′
II–4	12–06–82	2120	887	28°20′	89°27′
II–5	12–07–82	0715	885	28°20′	89°27′
II–6	12–07–82	1220	834	28°19′	89°25′
II–7	12–08–82	1820	443	28°32′	89°53′
II–8	12–09–82	0830	402	28°34′	89°53′
II–9	12–09–82	1215	461	28°32′	89°53′
II–10	12–13–82	1245	44	29°26′	85°53′
II–11	12–15–82	1930	19	28°54′	89°29′
II–12	12–16–82	0900	68	28°51′	89°32′
III–1	11–19–83	1200	27	28°54′	89°29′
III–2	11–20–83	0800	35	28°47′	89°59′
III–3	11–20–83	1946	732	28°38′	89°00′
III–4	11–21–83	0555	27	28°54′	89°30′
III–5	11–22–83	1100	48	28°51′	89°30′
III–6	11–23–83	0500	194	28°31′	89°37′
III–7	11–24–83	1030	50	28°50′	89°31′
III–8	11–25–83	0820	45	28°55′	89°34′
III–9	11–25–83	1945	40	28°56′	89°36′
III–10	11–26–83	1200	16	28°54′	89°29′
III–11	11–27–83	0900	9	29°02′	89°30′
III–12	11–28–83	0840	29	28°48′	89°57′
III–13	11–28–83	1250	44	28°56′	89°51′
III–14	11–29–83	0950	24	29°03′	89°39′
III–15	11–30–83	0930	44	28°47′	89°58′
III–16	12–01–83	0800	38	28°52′	89°29′
IV–1	3–14–83		53	27°58′	95°53′
IV–2	3–19–83		59	28°18′	90°41′
V–1	2–21–84	0850	18	28°54′	90°25′
V–2	2–22–84	0830	18	28°54′	90°25′
V–3	2–23–84	0910	18	28°54′	90°25′
V–4	3–1–84	0835	18	28°54′	90°25′
V–5	3–1–84	0830	18	28°54′	90°25′
V–6	3–3–84	0730	18	28°54′	90°25′

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

[5]Multiple opening-closing net and environmental sensing system.

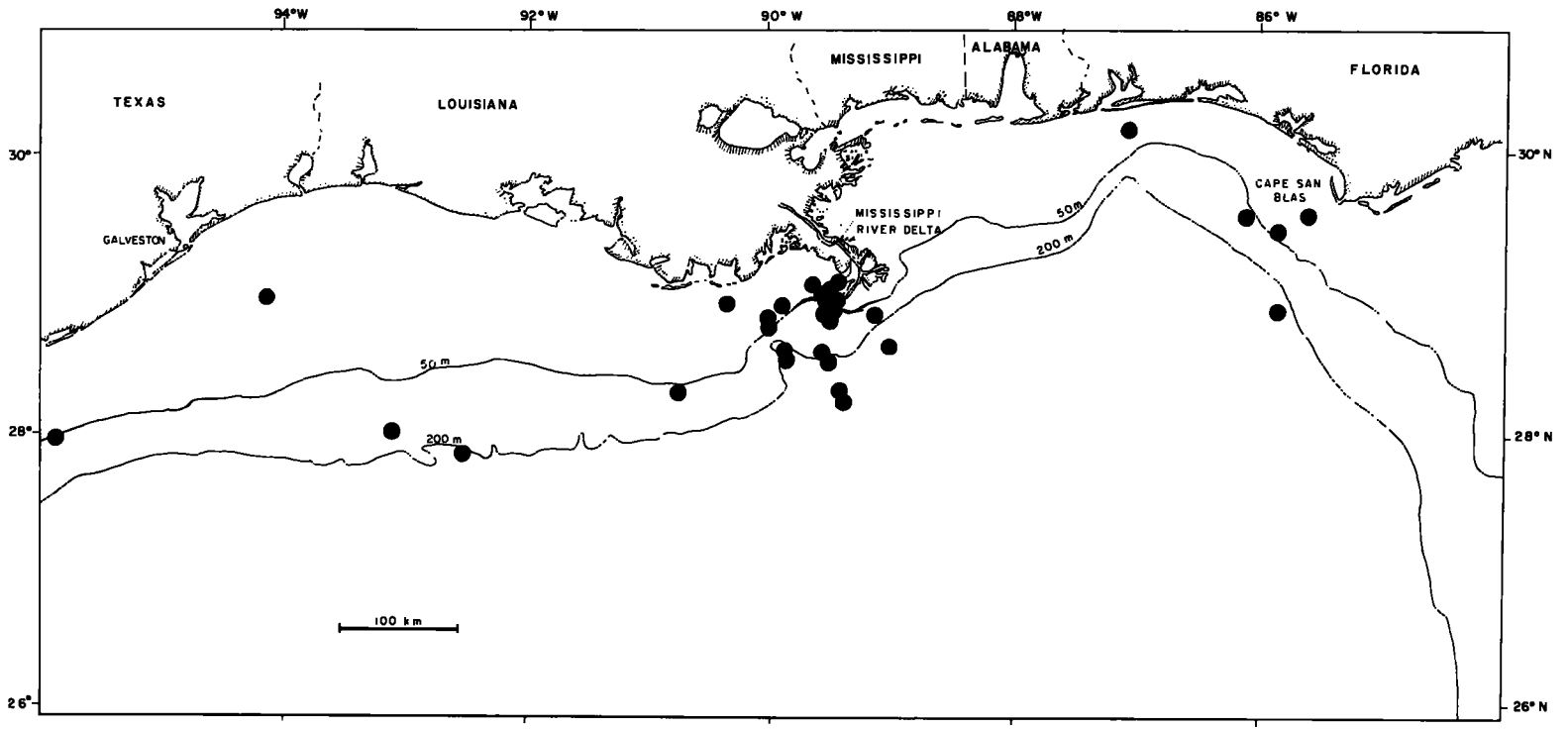

FIGURE 1.—Station Locations.

ments. On cruise IV, a Plessey Model 9040 CTD was used for both temperature and salinity. On cruise V, salinity samples were stored in bottles and analyzed in the laboratory using a Guildline Model 8400A Autosal, and temperature was measured with reversing thermometers.

Microzooplankton were collected using 5 L (cruises I, II, and V) or 30 L (cruises III and IV) Niskin bottles. During cruise I, 1 L samples of untreated water were collected from 3 depths and preserved for later analysis. During subsequent cruises, samples were collected from up to 8 depths; four liters were poured gently through a 20 μm sieve, backwashed with filtered seawater into a sample jar, and preserved in a 5% formalin-seawater solution. In the laboratory, all organisms in each preserved sample were identified and counted. In selected samples, the length and width of the first 50 copepod nauplii were measured using an ocular micrometer. In addition, during cruise I larger nauplii were collected with 0.1 m^2 64 μm mesh nets nested inside the 1 m^2 333 μm mesh nets of a MOCNESS net (Wiebe et al. 1976). Estimates of naupliar abundance from these collections were used separately in the analyses for patterns in distribution and abundance. Lastly, from cruise I, the total number of copepods in the shallow-water samples, total number of copepods from the 333 μm nets, and the zooplankton displacement volume from the 333 μm nets were analyzed for patterns in distribution and abundance.

RESULTS

Samples from the Mississippi River delta region, collected during 1981 (cruise I), 1982 (cruise II), and 1983 (cruise III), were compared to determine if there was significant interannual variability within a region. Whole water samples and samples retained on 20 μm mesh sieves were pooled for this analysis under the assumption that nauplii in a whole water sample would be retained on a 20 μm mesh screen. The 64 μm net samples were excluded from this analysis. This test was made using average naupliar concentrations in the upper 10 m only; naupliar concentrations were typically lower in deeper waters, and we did not have the same number of deep and shallow stations for each of the 3 sampling years. A 1-way analysis of variance indicated significant variation between years within the Mississippi River delta region ($P < 0.01$). All 3 years were statistically different. These results indicated to us that regional or other spatial comparisons can only be made using samples collected during the same year. Interannual comparisons for other regions were not possible.

Samples were collected from all 3 regions during cruise I. Four tests for regional differences during this cruise were made. First, regions were compared based on naupliar concentrations in the upper 10 m only (Table 2); based on whole water collections F was significant at $P < 0.05$ and based on samples collected with 64 μm mesh nets F was significant at $P < 0.09$. Second, regions were compared based on naupliar concentrations from all depths (Table 2); based on whole water collections F was significant at $P < 0.01$ and based on samples collected with 64 μm mesh nets F was significant at $P < 0.22$. Thus, whole water samples collected on cruise I indicated significant regional differences in naupliar concentration but samples collected with 64 μm mesh nets did not. In addition, there were significant regional differences in the concentrations of total copepods ($P < 0.01$) and in zooplankton displacement volume ($P < 0.05$) during cruise I (data not shown). Regional comparisons were not possible during other cruises because all 3 regions were not sampled in years other than 1981.

Where possible, we also tested for onshore-offshore gradients in naupliar concentrations in the upper 10 m. Stations were categorized according to bottom depth as shallow, <18 m, intermediate, 18–90 m, and deep, >90 m, and comparisons were made between these 3 depth categories. A highly significant onshore-offshore difference existed during cruise I for nauplii collected with the 64 μm MOCNESS nets (Table 3). During cruise III samples were only collected in the Mississippi River delta region but onshore-offshore differences within this region were significant (Table 3). No significant onshore-offshore gradients were observed in naupliar concentrations determined from whole water samples collected from all 3 regions during cruise I, or in nauplii from only the Mississippi River delta region during cruise II (Table 3).

Although regional differences in average concentrations of nauplii were not strong, the vertical distributions were different. For example, several stations at approximately the 50 m isobath are compared in Figure 2. At station IV-1 (Fig. 2a) off the coast of Texas, there was no marked vertical heterogeneity in naupliar concentrations, the maximum concentration was low (23 nauplii/L), and the average concentration was

TABLE 2.—Regional comparisons of naupliar concentrations during cruise I. Samples were collected by 2 methods: whole water samples were collected with Niskin bottles, and 64 μm mesh nets were used to collect the net caught samples.

Cruise	Depths	Sample type	*n*	Probability of *F*
I	upper 10 m	whole water	28	< 0.05
I	upper 10 m	64 μm nets	126	< 0.09
I	all depths	whole water	57	< 0.01
I	all depths	64 μm nets	222	< 0.22

TABLE 3.—Onshore-offshore comparisons of naupliar concentrations from the upper 10 m of each station. Tests for cruise I are based on naupliar concentrations from all 3 regions pooled then separated into 3 depth categories. During cruises II and III, nauplii were only collected from the Mississippi River delta region.

Cruise	Regions	Sample type	*n*	Probability of *F*
I	all	whole water	28	< 0.14
I	all	64 μm nets	126	< 0.01
II	Mississippi R.	20 μm sieve	28	< 0.25
III	Mississippi R.	20 μm sieve	49	< 0.01

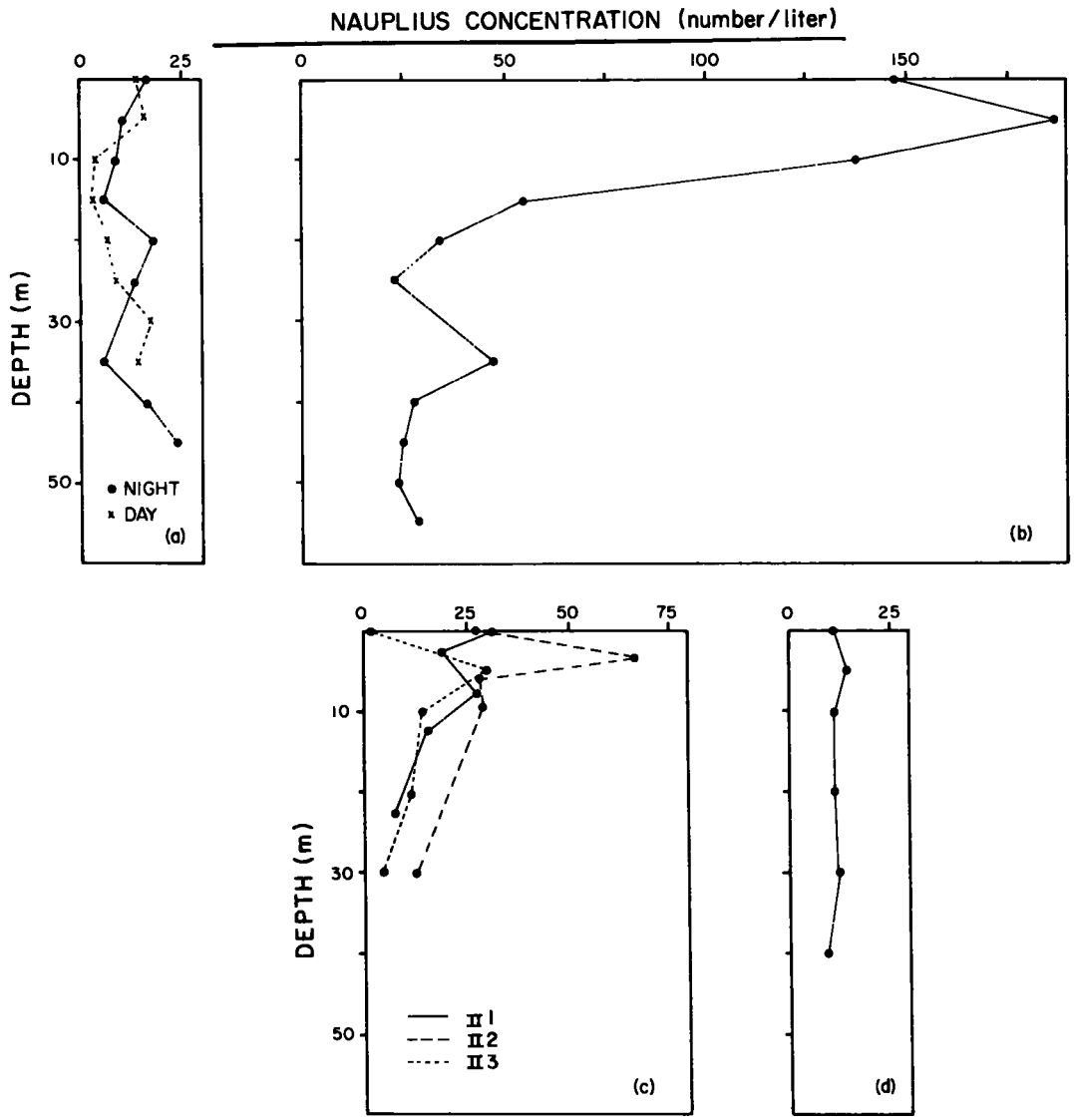

FIGURE 2.—Naupliar concentrations (number/liter) from selected stations near the 50 m isobath on the Texas continental shelf (a, station IV-1), the Louisiana Shelf (b, station IV-2, c, stations II-1, II-2, II-3), and the northwest Florida shelf (d, station II-10).

low (11 nauplii/L). The same pattern was observed off Cape San Blas (Fig. 2d); there was no marked vertical heterogeneity, and the maximum and average concentrations were low, 14 and 12 nauplii/L. In contrast, nauplii at stations near the 50 m isobath in the region near the Mississippi River delta typically showed marked vertical heterogeneity in abundance. At station IV-2 (Fig. 2b), the maximum concentration was 187 nauplii/L and the minimum was 24 nauplii/L. At station II-1, II-2, and II-3 in the Mississippi River delta region (Fig. 2c) naupliar abundances were also vertically heterogenous, although concentrations were lower than at Station IV-2. In general, based on all our vertical profiles (most not shown), regions influenced by the Mississippi River can contain high concentrations of nauplii in the surface layer, while subsurface concentrations are similar to concentrations in the other 2 regions.

Vertical structure in the distribution of nauplii appears to be related to physical structure. At the stations off the coasts of Texas and Florida (Fig. 2a, 2d), temperture and salinity were essentially vertically homogenous (Fig. 3a, 3d) whereas off the Mississippi River delta temperature and

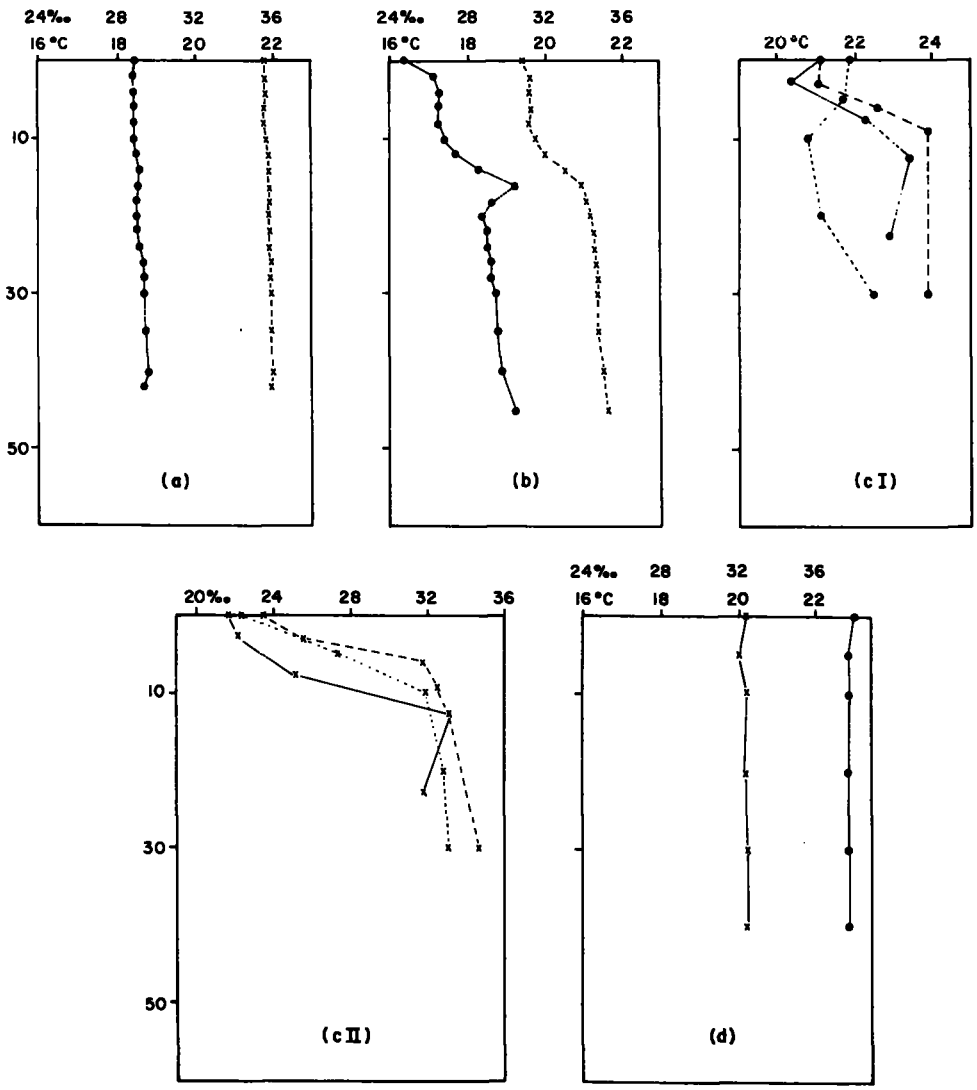

FIGURE 3.—The vertical distribution of temperature (•) and salinity (×) at the stations represented in Figure 2.

salinity were vertically stratified (Fig. 3b, 3c). The same pattern was seen in the chlorophyll a distributions (Fig. 4) and the nitrate distributions (Fig. 5).

Correspondence between chlorophyll a concentration and naupliar abundance was computed; the correlation coefficient for a linear regression of chlorophyll concentration on naupliar abundance for all 5 cruises (n = 269) was 0.39, significant at the 1% level. However, analysis of covariance showed that the relationship between chlorophyll and naupliar concentration was significantly different between cruises, and therefore the data from the 5 cruises should not be pooled. Although a significant relationship between chlorophyll concentration and naupliar concentration typically exists, it is not consistent from cruise to cruise. Regression parameters and correlation coefficients for each cruise are shown in Table 4. Pairwise tests indicate that the slope of the regression for cruise V was significantly different from all the others, cruise IV was differ-

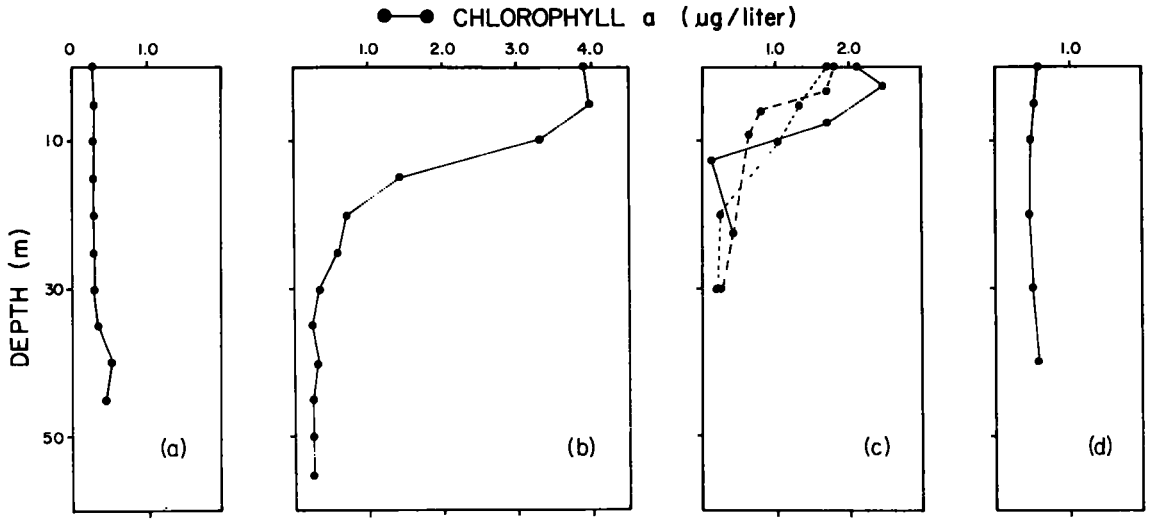

FIGURE 4.—The vertical distribution of chlorophyll a at the stations represented in Figure 2.

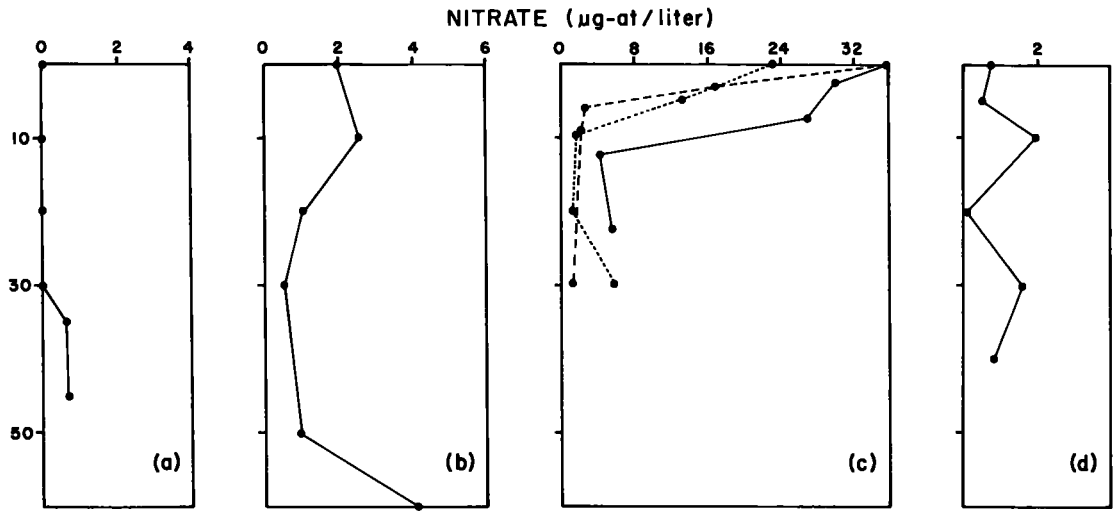

FIGURE 5.—The vertical distribution of nitrate at the stations represented in Figure 2.

TABLE 4.—Parameters and coefficients for linear regressions of chlorophyll concentration on nauplius concentration for each cruise. $Y = a + b(X)$ where Y = naupliar concentration as number per liter, and X = chlorophyll concentration as μg per liter. Significance level tested is 0.01.

Cruise	n	Intercept	Slope	Significance of slope	r^2	Significance of correlation
I	57	12.9	9.7	<0.01	0.40	<0.01
II	70	5.4	15.4	<0.01	0.53	<0.01
III	80	3.7	9.2	<0.01	0.34	<0.01
IV	20	6.9	39.4	<0.01	0.94	<0.01
V	42	26.1	1.1	NS	0.04	NS

ent from all others, cruise II was different from all the others, and cruises I and III were not different from each other but different from cruises II, IV, and V. The slopes of all relationships except cruise V were significantly different from zero.

The size-frequency distribution of nauplii did not vary in any systematic manner (Fig. 6). For example, at station IV-1, the bulk of the nauplii were between 20 and 100 μm at all depths sampled during both the daytime and nighttime periods. The size-frequency distribution was essentially identical at station IV-2, off Louisiana (data not shown).

At some stations, copepodid stages <600 μm in length (50–200 μm in width) were counted in addition to nauplii because they are potential prey items for menhaden larvae. Copepodites were usually not as abundant as nauplii, especially at stations with high naupliar abundances. On occasion, they were as abundant or, at specific depths, more abundant than the nauplii (Table 5). The ratio of nauplii to copepodites varied widely, between 16.3 and 0.3, so it is not possible to assign a constant factor to naupliar abundances to estimate the increase in available prey attributable to copepodid stages.

Other microzooplankton were usually not as abundant as nauplii or copepods. In our samples, various forms of eggs reached a maximum density of 6 eggs/L (cruise III station 6 at 3 m, data not shown). Pelecypod larvae at one station (III-11) were abundant, reaching a maximum of 29 larvae/L at 4 m, compared with 22 nauplii, 7 copepodites, and 2 eggs/L in the same sample. Only on this one occasion were organisms other than copepodites or nauplii the dominant form of microzooplankton.

TABLE 5.—Abundance (number/liter) of other microzooplankton in addition to nauplii at selected stations during cruise III.

Station	Depth (m)	Nauplii	Copepodids <600 μm	Copepodids >600 μm	Larvaceans	Eggs	Other
III–3	6	17.3	7.5	1.0	7.8	0.5	1.8
	9	29.3	12.0	0.5	11.0	0	1.8
	12	17.5	8.0	1.0	6.8	1.5	2.3
	20	7.8	2.8	0	1.0	2.0	0.5
III–7	0	24.0	6.3	4.0	0	1.0	1.0
	3	15.3	12.3	1.0	0	0.3	1.3
	5	3.0	5.0	1.0	0	0.8	0.3
	13	4.8	5.8	0.3	0	0	0.5
	22	2.0	1.0	0.3	0	0	0
III–14	0	15.8	12.0	1.3	0	1.3	2.0
	5	44.8	3.8	0.3	0.5	3.0	4.0
	10	40.0	6.8	0.8	1.3	4.3	0.3
	15	11.5	8.0	3.8	1.0	1.8	0.3
	20	12.0	35.0	6.8	0.3	0.3	0.8
III–16	0	15.8	25.3	5.0	0	0	12.8
	6	8.0	16.0	2.3	0	1.0	2.5
	9	30.0	14.0	2.0	0	0.3	2.5
	12	29.0	13.3	0.5	0	0.8	1.3
	15	17.0	12.5	1.0	0	0.8	0.5
	25	31.8	12.8	0.8	0	0	5.0

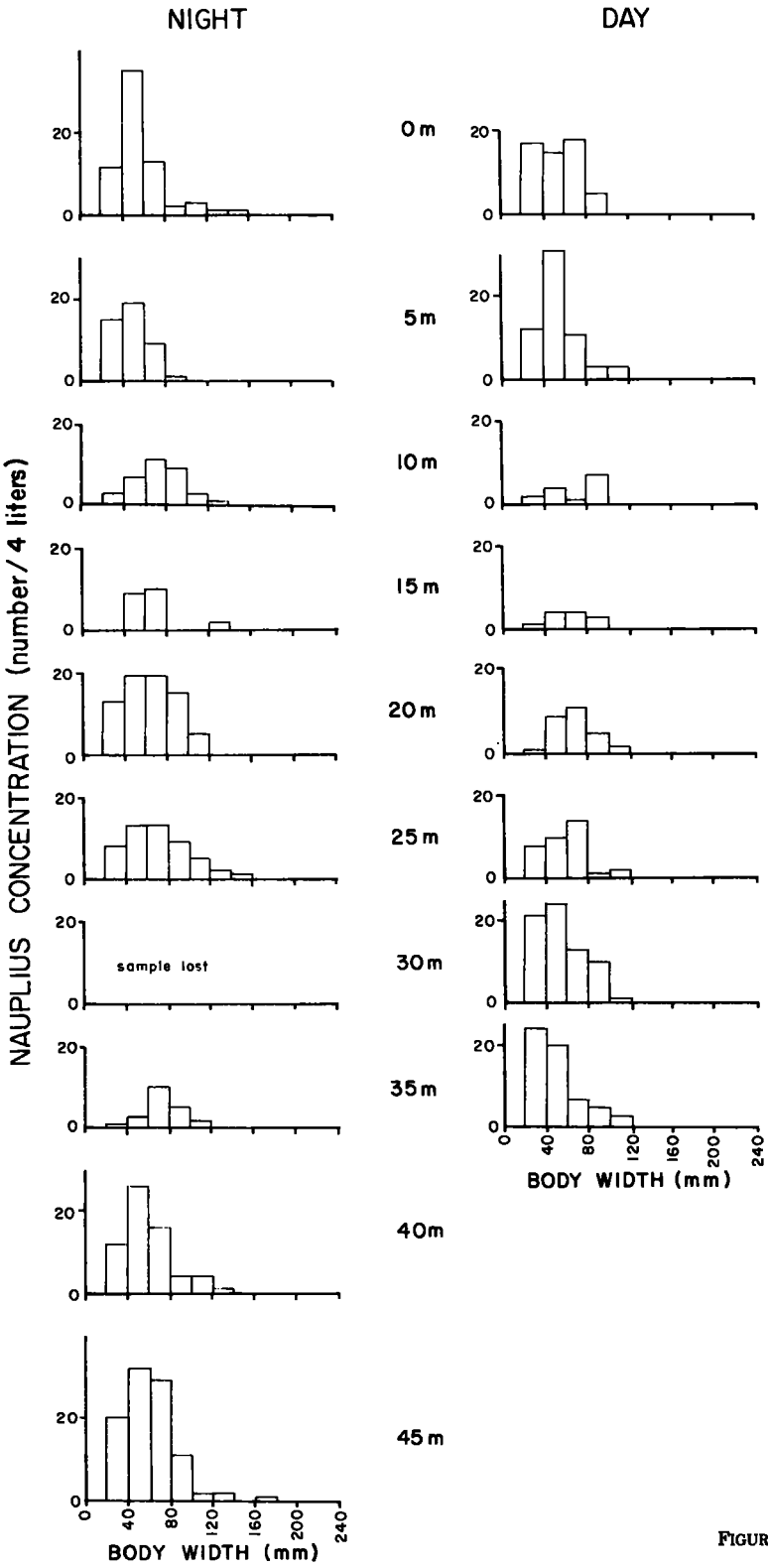

FIGURE 6.—The size-frequency distribution of nauplii from station IV-1.

DISCUSSION

Menhaden larvae between 3 and 20 mm long collected during wintertime from 3 regions in the northern Gulf of Mexico contained a variety of diet items, including dinoflagellates, tintinnids, copepod eggs, nauplii, copepodids, juvenile pelecypods, and pteropods (Govoni et al. 1983, 1985). Dinoflagellates and tintinnids constituted the main diet items of larvae <5.0 mm long but were replaced by copepod nauplii, then copepodids and small adult copepods as larvae grew larger.

In another study, Stoecker and Govoni (1984) found that copepod nauplii were the dominant items in the diet of menhaden larvae 7.0–9.0 mm long, although only 12 fish were examined. Later studies, however, have verified that nauplii are the dominant items in the diet of a wide size range of larval menhaden collected in the boundary between the plume of the Mississippi River and oceanic waters (Govoni and Hoss fn. 3)

The maximum width of food items in menhaden larvae <5 mm long was about 200 μm (Govoni et al. 1983). This width increased up to about 400 μm for larvae 10 mm long. In another study (Stoecker and Govoni 1984) maximum prey size was calculated in a different manner; the average width of the largest prey type was used. With this index the estimated maximum width of prey items was 50 μm for larvae <5 mm long and about 140 μm for larvae 9–11 mm long. In our study, most of the nauplii were between 40 and 80 μm body width, and most of the copepodites were between 50 and 200 μm body width. These copepod developmental stages were in the size range of diet items typically found in guts of intermediate size (7–11 mm) larvae of the gulf menhaden and we believe our samples are reasonably representative of the prey concentrations available to these larvae. Other prey items for larvae in this size range were common only on rare occasions.

The importance of high prey concentrations to successful feeding and survival of fish larvae has frequently been noted (Hunter 1981). Concentrations required to give high survival in laboratory experiments are seldom found in the ocean but careful attention to culture techniques can result in reasonably high survival at prey densities that are close to or overlap the maximum natural concentrations (Houde 1978). At stations near the river delta that are strongly affected by the river plumes, maximum concentrations of nauplii were typically in the range of 20–50 nauplii/L. At stations farther down plume, away from the delta, maximum naupliar concentrations were higher, up to 187 nauplii/L at station IV-2 for example. It is not clear whether this is a seasonal pattern, a pattern due to the down-plume development of the food web, or a pattern attributable to some other factors. However, the concentrations observed in waters with salinities lowered by the river plumes are mostly within the range of 10–100 nauplii/L that is frequently reported for oceanic and coastal waters for microzooplankton, or the 50–100 nauplii/L range for coastal and estuarine areas (see Houde 1978; Hunter 1981 for summaries). The addition of copepodite stages and other potential prey items to the naupliar abundances in this study would increase the estimates of available prey somewhat but usually not more than 20%. At least during the wintertime, the waters surrounding the Mississippi River delta do not appear to contain exceptionally high concentrations of copepod nauplii, compared to other coastal and estuarine areas.

The vertical distribution of nauplii was frequently similar to that of chlorophyll. Regressions of naupliar concentration on chlorophyll concentration were significant for 4 of the 5 cruises although not the same in each case. Assuming chlorophyll is a reasonable indicator of phytoplankton abundance and thus food abundance for nauplii, then nauplii appear to be aggregated at the depth of highest food availability. Year to year variability in the relationship indicates that other factors are also important in determining the abundance and distribution of nauplii. Because eggs released from adult female copepods would sink out of the surface water before hatching, it is probable that active swimming by nauplii plays a part in the aggregation process, perhaps enchanced by physical convergence processes.

In our study we noted that there were interannual differences in naupliar concentrations, there were sometimes significant regional differences, and there were sometimes significant onshore-offshore differences. Although we anticipated finding higher concentrations of nauplii in the region near the Mississippi River delta, this pattern was not always observed. This finding might indicate that there is not an important difference between the 3 regions as far as larval food availability is concerned. Alternatively, it might indicate that there are subregions within the larger Mississippi River delta region that contain a food environment for fish larvae that allows for enhanced survival and growth, but that we failed

to clearly identify and segregate these regions. The overall region did not always appear significantly better than the other regions because only parts of it are better.

On the continental shelf in the Gulf of Mexico, as in other shelf regions of the United States, the typical pattern is for the water to be vertically well-mixed during the wintertime (Parker 1968). Autumn cooling breaks down the thermal stratification that has existed throughout the summer and allows the isothermal water column to be easily mixed. The major exception to this general pattern in the Gulf of Mexico is the shelf region influenced by the large volume of freshwater runoff from the Mississippi River. During this period, the freshwater influx is of sufficiently large volume (average flow for December to March in 1975 through 1979 was 17,290 m^3/second (U.S. Army Engineer District, New Orleans Corps of Engineers, 1980)) to physically stratify the shelf waters hundreds of km downstream from the delta. We suggest that this salinity-induced stratification is a vital component of the recruitment success of Gulf menhaden because it provides an environment in which prey aggregations can occur. It has been suggested that vertical stratification by other small-scale physical phenomena (e.g., Langmuir circulation) allows significant patchiness of prey items to exist (Lasker 1975). This patchiness provides small regions of comparatively high food concentrations for fish larvae, and results in improved feeding success. In this study, copepod nauplii were aggregated vertically at stations with physical stratification and were nearly homogenously distributed at stations lacking physical stratification. Maximum naupliar concentrations (no. per m^3) at stratified stations were typically 2–10 times greater than at non-stratified stations.

In conclusion, we believe that the large freshwater inflow of the Mississippi River during the wintertime spawning period of the Gulf menhaden contributes to the feeding success and survival of larval fish by providing physical stratification which in turn results in a vertical stratification of phytoplankton and microzooplankton in layers or patches of relatively high concentrations.

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A LIMITED INFORMATION APPROACH FOR DETERMINING CAPITAL STOCK AND INVESTMENT IN A FISHERY[1]

JAMES E. KIRKLEY[2] AND DALE E. SQUIRES[3]

ABSTRACT

There have been few empirical studies on the level of capitalization and investment in fisheries because the necessary data are often inadequate. Specifically, data on capital stock and investment in a fishery are not routinely collected and compiled or are limited in scope. In this study, a method is provided for estimating the aggregate capital stock and investment in a fishery utilizing the available information. Data on acquisition and list prices and vessel characteristics for a sample of New England vessels are obtained. The data are then used to estimate an hedonic cost function which specifies the acquisition price as a function of vessel characteristics. The resultant equations are subsequently used, with information on vessel characteristics for all New England vessels, to estimate aggregate capital stock and investment. The results indicate that substantial investment occurred in the otter trawl and scallop dredge fisheries, particularly since the Magnuson Fisheries Conservation and Management Act. Moreover, the results demonstrate that the number and change in the number of vessels are inadequate indicators of the level of capital stock and investment in a fleet comprised of vessels with heterogeneous characteristics.

The common property nature of fisheries is recognized as causing excess capitalization and harvesting capacity (Gordon 1954). The theoretical argument is that since fishermen do not have to pay for the utilization of common property fish stocks, new vessels enter a fishery until net revenue is driven to zero. This common-property feature results in more capital and investment than is economically optimum. Public regulation of fishing industries is usually advocated to redress the excess entry, economic inefficiency, and loss of economic rents in a common property fishery (Scott 1979; Sissenwine and Kirkley 1982).

In essence, overcapitalization and excess investment are perceived to be the reasons for many of the major fisheries problems (Hilborn 1983). Economists argue that management of overcapitalization is necessary to realize the benefits of fisheries (Cunningham et al. 1985). Alternatively, gains from fisheries management require control of overcapitalization and excess investment (Charles 1983a, b).

Clark et al. (1979) and Charles (1983a, b) extended the static theory of optimal fisheries investment as developed by Gordon (1954). They also demonstrated the relationships between investment, capital stock, overexploitation, and fisheries management. They concluded that investment should be more conservative to prevent overexploitation.

The economic literature provides substantial justification for the need to solve the problems of overcapitalization and excess investment. Yet, few empirical studies document the level of capitalization and investment.[4] Moreover, there appears to be no attempt by any U.S. agency to routinely collect and compile statistics on either the stock of capital or the level of investment in U.S. fisheries. Overcapitalization and excess investment, though, continue to be suggested as the reasons for many of the economic problems of fisheries.

Since data are often inadequate, many empirical studies on fisheries consider capital stock and investment in terms of the number of vessels. That is, capital stock and investment in a fishery are tyically measured in terms of number of vessels. In the absence of appropriate information, the number of vessels may be the only basis for examining overcapitalization and excess investment. Alternatively, if a fleet has identical-sized vessels, fixed inputs or vessel characteristics, and

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[4]Tettey et al. (1986) provided an exception, but their analysis is restricted to the shrimp fishery and is based on cost data obtained from boat builders.

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gear, the number of vessels may be used to indicate the stock of capital and investment. However, Kendrick (1961) demonstrated that the total number of operating units, such as the number of plants, is an inadequate measure of capital stock. Also, few fleets have identical-sized vessels, characteristics, or gear. As a consequence, the number of vessels does not provide adequate information to indicate the level of capitalization and investment.

This study presents an approach for estimating the aggregate or industry level of capital stock and investment in a fishery comprised of heterogeneous vessels using available information. Data available include acquisition and list prices for some but not all vessels and boat characteristics for all vessels in a fleet. The approach was developed and used to obtain estimates of capital stock in support of the United States and Canadian maritime boundary dispute. It is viewed as an initial step towards examining the problems of excess capitalization by providing estimates of aggregate capital stock and investment.

THE DEFINITION AND MEASUREMENT OF CAPITAL AND INVESTMENT

Capital

The concept of capital has created problems for economists for quite some time. The term has been used in so many different contexts that it is a source of enormous confusion (Hirshleifer 1970). Sloan and Zurcher (1968), in their "Dictionary of Economics", define capital as "One of the major factors of production consisting of property from which an income is derived, expressed in terms of money. Popularly, the term is frequently used interchangeably with capital good. A distinction is sometimes made between money capital, or that part of the capital held in the form of money and bank deposits, and property capital, or that part of the capital held in the form of evidences of ownership such as stocks, bonds, and mortages."

Hirshleifer (1970) presented three meanings of capital: 1) real capital or capital stock, 2) capital value, and 3) liquid capital. Real capital is defined as a collection of capital goods or an aggregate of heterogeneous capital inputs. It is one of the major productive commodities or economic factors of production. Capital value is the net discounted value of expected future income streams associated with a capital good. Liquid capital is the level of current funds available or intended for investment.

In the case of fisheries, real capital or capital stock is the form of capital which should be examined with respect to the problems of overcapitalization and excess harvesting capacity. It is the relevant measure of capital goods used or available for production (National Academy of Sciences 1979). Moreover, capital stock is the concept of capital used to define and measure the services of capital inputs which are required to harvest fish; that is, it is the concept of capital required to define the economic production technology of a fishery. Thus, this study is concerned with the concept of real capital stock.[5]

The measurement of capital stock in a fishery, however, presents several problems. First, capital inputs are usually quite heterogeneous and cannot be easily aggregated without restrictive assumptions about the form of the catch equation or fishermen's behavior. Conceptually, it should be possible to combine all the different types of capital goods by weighting each type by its average compensation (i.e., the rental price). However, information at this level of detail is typically not available. Second, fisheries agencies, particularly in the United States, generally do not collect and compile information necessary to calculate capital stock and investment. Third, in order to compare changes in capital stock over time, the measure of capital stock must be converted to some base period value by deflation.

In empirical economic studies of traditional industries, the common practice is to measure the capital input or stock by converting the purchase or acquisition price or the book values of capital to base period values by the use of a price index (National Academy of Sciences 1979). Varian (1984) noted: "The usual procedure is to measure capital value and then deflate by a price index; in some sense, this should measure the level of capital stock." In this study, the acquisition price is used as the measure of the stock of capital or capital value; the real stock of capital is obtained by dividing the capital value by the producer price index for heavy machinery.

Investment

The definition and measurement of investment is more straightforward than is the definition and

[5]The market value of capital, acquisition price, and cost of capital are used interchangeably in this study.

measurement of capital. In simple terms, investment is the exchange of money for some form of property. Although there are several types of investment (Branson 1972), attention is restricted in this study to an examination of net investment (i_n) which is defined as the difference between the stock of capital in two periods of time (Baumol 1977). This is the same concept of investment examined by Tettey et al. (1986).

Replacement investment is another type of investment. The sum of replacement investment and net investment equals total investment. Replacement investment is measured by multiplying the rate of depreciation times the level of the capital stock. Replacement investment, however, is not estimated in this study since the method and rate of depreciation must be arbitrarily assumed.

METHOD OF ANALYSIS

The Hedonic Approach

While the definition and measurement of real capital stock and investment are conceptually straightforward, limited data and heterogeneous capital inputs complicate the measurement of capital stock and investment. In particular, data are usually only available for a small number of vessels which are often similar in their characteristics; these data are inadequate for calculating actual or observed capital stock and investment in a fishery. However, data are available on the acquisition price and characteristics of vessels which permits estimation of the stock of capital by an hedonic approach. In turn, estimates of capital stock from the hedonic approach can be used to estimate net investment in a fishery.

The hedonic approach hypothesizes that the price of a commodity is influenced by its characteristics (Rosen 1974). The hedonic price or characteristics function in market equilibrium reflects both the distribution of marginal rates of substitution over households and the distribution of marginal rates of transformation over firms. In effect, the hedonic hypothesis states that goods may be valued for their attributes and that implicit or hedonic prices exist as a function of the attributes.

Griliches (1971) estimated hedonic cost functions of U.S. automobiles using advertised or list prices and actual transaction prices. Griliches, however, was concerned with explaining quality differentials. Ladd and Martin (1976) examined prices and demands for input characteristics using a Neoclassical input characteristics model. Triplett (1986) estimated quality adjusted price indexes for computers. Thus, there is a history of deriving prices of commodities as a function of their characteristics.

The hedonic approach offers several attractive properties for estimating capital stock in fishing industries. First, the hedonic method incorporates changes in the quality of capital over time (Triplett 1986). This is because changes in quality should be reflected in vessel acquisition prices. The hedonic approach, thus, permits a quality adjusted measure of capital stock to be obtained. In contrast, vessel count ignores changes in the quality of capital. Second, the hedonic approach allows easy aggregation of the heterogeneous capital inputs frequently observed in a fishing fleet because the heterogeneous capital is measured by value rather than physical measures.

In the hedonic approach, cost (C) or input price may be expressed as a function of the associated characteristics of the commodity or input,

$$C = f(CH_1, CH_2, \ldots, CH_n) , \qquad (1)$$

where C is cost, CH_i is the ith characteristic (Braeutigam et al. 1982). The characteristic cost equation can be obtained either from a dual specification or by determining the reduced form equilibrium equation.

The Dual and Reduced Form

The dual specifies cost as a function of input prices and their characteristics. The partial derivative of the dual cost function with respect to input prices yields the demand for the inputs as a function of prices and input characteristics. The reduced form is obtained by solving structural equations, equations which explain the behavior and interrelations of endogeneous variables, of demand and supply for the endogeneous variable, price, in terms of exogeneous variables and disturbance terms.[6]

In this study, the reduced form is directly specified and estimated for two reasons: First, all of the input price data necessary for estimating a dual are not available. Second, estimation of the structural equations is complicated by the need to use a limited dependent variable method of estima-

[6]See Rosen (1974) for additional information on obtaining reduced form equations for hedonic prices.

tion since demand is a discrete choice, and there are individuals or firms which do not purchase a vessel.

Rather than attempt to deal with these difficulties which do not appear to have widely accepted solutions, it is assumed that there are underlying structural equations of demand and supply which permit the derivation of the reduced form equation. Moreover, the direct specification and estimation of the reduced form is the more commonly used approach to estimate the value of a commodity as a function of its characteristics (Bockstael et al. 1986). Last, the use of the reduced form should not create a problem since the hedonic function is a joint envelope in characteristic space of demander's bid schedules and sellers offer schedules, and thus, the observed implicit price locus is a reduced form equilibrium vector reflecting both supply and demand influences. As a result, shifts in both market demand and supply are incorporated into the reduced form equilibrium vector.

The Capital Stock Model

As previously indicated, it is common practice to use the acquisition price as a measure of capital stock. By the hedonic approach, the capital stock or acquisition price of a fishing vessel is postulated to be a function of several vessel characteristics. The following general specification is considered:

$$C = f(LN, CS, YEAR, FI, AGE, DNO, HPWR, GRT), \quad (2)$$

where C is the list or advertised price or the acquisition price of a vessel, LN is length, CS is hull type (1 = steel, 0 = other), FI is fishery or gear type,[7] AGE is age of vessel, DNO is a dummy variable for new and used vessels (DNO = 1 for new and 0 for used), HPWR is engine horsepower, and GRT is gross registered tonnage. The variable year equals the year of the observation. It is included to incorporate technological changes over time, such as the introduction of electronics and stern trawling, and structural changes in the industry such as changes in organization of capital and fish markets and changes in public regulation.

[7]Gear type is an integer valued variable set equal to the gear codes used by the Northeast Fisheries Center. This may influence the results similarly to the use of nonbinary dummy variables (Kmenta 1971). The use of this variable implies that the cost difference between gear types is equal to a scalar multiple of the lowest integer valued gear code. Thus, statistical rejection of cost differences due to gear type is actually a rejection of differences not being equal to scalar multiples. However, the large number of gear codes prohibits their separate treatment.

Functional Form

Several functional forms could be specified for Equation (2). Alternatively, generalized Box-Cox (Box and Cox 1962) transformations could be used to determine the functional form. However, the selection of functional form is mostly concerned with obtaining the relationship between the dependent variable and individual independent variables.This study is primarily concerned with estimating the capital stock. Moreover, it may be quite difficult to estimate capital stock from Box-Cox transformations or other functional forms since the conditional expectation is often of a complex form (Smallwood and Blaylock 1986). Also, Dadkhah (1984) noted that predictions based upon some transformations and functional forms result in biased predictions and asymmetric confidence intervals.

Since this study is primarily concerned with estimating capital stock and investment rather than estimating the implicit prices for characteristics, a linear functional form is proposed for Equation (2). The capital stock equation is specified as a second-order polynominal in order to provide an approximation to an unknown, underlying hedonic function. This is equivalent to specifying a generalized quadratic flexible functional form and imposing zero valued restrictions on the cross product coefficients or interaction terms (Lau 1978). Flexible functional forms are widely used in economic studies concerned with determining the underlying economic structure because they impose very little structure on the economic equations of concern (Blackorby et al. 1978).

Postulated Relations

The postulated relations between cost and each of the explanatory variables is as follows: 1) the coefficients for the first order terms of vessel tonnage, length, and engine horsepower should be positive since costs should increase as the size characteristics increase; 2) the coefficient for steel-hulled vessels should be positive since steel vessels are generally more expensive than wood or fiberglass vessels; 3) the dummy variable coef-

ficient for new vessels should be positive since new vessels tend to cost more because they are newer and usually incorporate more recent technological advances; 4) the second-order coefficients for the size characteristics are expected to be negative since cost is believed to increase at a decreasing rate in response to increases in the size of a vessel.

THE DATA

Data used to estimate the capital stock equation were obtained from three sources: First, information on vessel acquisition price and associated characteristics were obtained for 164 new vessels from the Northeast Regional Office of the National Marine Fisheries Service.[8] Second, data on list prices and vessel characteristics for 946 used vessels were obtained from various trade magazines and vessel brokers. Third, detailed vessel and fishery data were obtained from the U.S. Coast Guard master vessel listing and the Northeast Fisheries Center. Data were obtained for the years 1965 through 1981.

The first two sets of data were used to estimate the capital stock equations. The third data set was used to estimate aggregate capital stock and investment in selected New England fisheries using the estimated capital stock equations; that is, vessel characteristics for all of the vessels in the New England fleet were inserted into the estimated capital stock equations to obtain estimates of capital stocks per vessel in a given year. The estimated capital stock per vessel was summed over all vessels in a year to obtain total or aggregate capital stock. Net investment was then calculated as the annual change in total capital stock.

The use of both the list and acquisition prices, however, presents a problem. The list price reflects the supply price or the price at which a vessel is offered for sale. The acquisition price reflects the price determined by the equilibrium between demand and supply. As a consequence, estimates of capital stock and investment may be in error.

It is not known by how much the acquisition price differs from the list price for used vessels. Thus, the magnitude of the error cannot be calculated. Since the list price is not less than the acquisition price, estimates of capital stock based on Equation (2) are likely upwards biased. Counter to this problem is the argument that by the time a vessel is ready for fishing, required capital modifications or improvements may result in the capital stock being close in value to the list price.

There are no completely satisfactory economic justifications for using both the list and acquisition prices. Two possible justifications are that Griliches (1971) and others used both prices, and capital improvements or modifications may be nearly equal to the difference between the list and acquisition prices. Another possible justification is the accepted use of cost data obtained from boat builders as in Griffin et al. (1978) which may impose similar problems plus the statistical problem of measurement error. In the remainder of this paper, the term "acquisition price" is used although the estimation and calculation of capital stock and investment are based on both price series.

EMPIRICAL RESULTS

Equation (2) was estimated by ordinary-least-squares with the dependent variable, the acquisition price, measured in both nominal and real terms; the real price is the nominal price deflated by the producer price index for heavy machinery. As previously stated, deflation is necessary to estimate the real capital stock. The estimated coefficients and statistical results are presented in Tables 1 and 2.

Equation (2), however, was also estimated using data for several groups of years between 1965 and 1981. The reason for considering different time periods was that prior knowledge of New England fisheries suggested that various changes occurred in the fisheries during the selected time periods.[9] Moreover, economic studies of New England fisheries have often been criticized for assuming stable relationships over time or over different cross sectional units. Failure to incorporate changes in the estimated relationship between cost and vessel characteristics over time may result in biased parameter estimates.

Changes which have possible ramifications for the estimated relationships include 1) depressed resource conditions and the presence of foreign fishing between 1965 and 1971; 2) management by the International Commission for Northwest

[8]Data are confidential and may not be available to other researchers or the general public.

[9]Additional information on possible structural changes in New England fisheries is available in Kirkley et al. (1982), Dewar (1983), Doeringer et al. (1986), and Kirkley (1986).

TABLE 1.—Parameter estimates of hedonic equation for nominal capital stock.

Years	N	Variables[1] Constant	GRT	GRT²	HPWR	HPWR²	LN	LN²	YEAR	DNO	FI	CS	AGE	R²
1965–71	133	13474.9	616.45	−5.25	−201.68	0.51	−208.99	11.46	−20.0	15692.2	−294.2	2315	−660	0.93
		[2](0.30)	(3.36)	(5.12)	(5.58)	(8.54)	(0.48)	(2.89)	(0.03)	(1.89)	(1.38)	(0.84)	(3.35)	
1972–75	216	−489183.0	−316.47	8.64	52.61	−0.13	6330.40	−59.33	4722.7	20176.7	−290.1	12117	−524	0.91
		(4.72)	(2.23)	(10.49)	(1.03)	(1.74)	(6.10)	(5.21)	(3.40)	(2.00)	(1.10)	(4.95)	(2.56)	
1976–77	164	−1755240.0	1,335.24	0.72	−60.09	0.16	6170.21	−56.79	20668.5	24038.5	968.7	12813	−749	0.85
		(3.58)	(4.30)	(0.61)	(0.65)	(1.65)	(4.24)	(4.04)	(3.17)	(1.82)	(1.96)	(3.07)	(1.83)	
1978–79	189	−3113870.0	673.62	−7.87	−116.75	0.44	1449.86	44.53	38888.1	2232.4	−259.4	13897	−6693	0.84
		(2.88)	(0.72)	(1.90)	(0.60)	(2.06)	(0.50)	(2.02)	(2.81)	(0.91)	(0.19)	(1.82)	(8.15)	
1980	271	−188637.0	261.24	0.99	224.79	−0.05	6059.50	−10.82	—	22818.2	1110.8	3969	−5867	0.89
		(2.22)	(1.52)	(0.56)	(1.65)	(1.33)	(2.09)	(1.49)		(1.93)	(1.87)	(1.44)	(9.25)	
1981	137	−50105.0	−4095.43	14.94	198.19	0.21	8208.01	−2.72	—	10463.9	75.6	34225	−9323	0.78
		(1.25)	(2.28)	(2.09)	(1.60)	(1.65)	(2.06)	(0.05)		(1.87)	(1.39)	(1.74)	(7.20)	
1965–81	1110	−528304.0	713.86	−0.22	−162.83	0.58	4054.12	−30.61	5967.9	45970.8	990.8	55730	−2217	0.82
		(7.04)	(2.05)	(2.15)	(1.57)	(5.25)	(2.47)	(2.28)	(6.20)	(3.59)	(1.42)	(4.60)	(4.08)	

[1]Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage and its value squared; 2) HPWR and HPWR² are engine horsepower and its value squared; 3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of observation; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwise); 6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.

[2]Numbers in parentheses are t-statistics.

TABLE 2.—Parameter estimates of hedonic equation for real capital stock, 1967 = 100.

Years	N	Variables[1] Constant	GRT	GRT²	HPWR	HPWR²	LN	LN²	YEAR	DNO	FI	CS	AGE	R²
1965–71	133	48304.1	724.35	−6.84	−219.74	0.54	−388.90	13.86	−500.2	18111.3	−273.8	2610	−653	0.89
		[2](1.01)	(3.74)	(6.33)	(5.76)	(8.72)	(0.85)	(3.28)	(0.73)	(1.97)	(1.21)	(0.90)	(3.15)	
1972–75	216	−81500.3	−185.96	5.18	32.62	−0.07	4009.60	−36.21	−117.8	13187.6	−213.9	8451	−411	0.90
		(1.17)	(1.96)	(9.37)	(1.05)	(1.61)	(5.75)	(4.73)	(0.13)	(1.94)	(1.21)	(5.15)	(3.00)	
1976–77	164	−782782.0	738.59	0.47	−31.06	0.08	3518.20	−32.20	8924.9	12827.3	559.8	11198	−422	0.83
		(2.88)	(4.28)	(0.71)	(0.60)	(1.18)	(4.35)	(4.13)	(2.46)	(1.98)	(2.04)	(3.11)	(1.95)	
1978–79	189	−1024330.0	331.40	−3.76	−59.41	0.21	897.93	19.14	12618.4	1074.3	−144.4	6882	−3147	0.81
		(2.02)	(0.75)	(1.94)	(0.65)	(2.16)	(0.66)	(1.85)	(1.95)	(0.09)	(0.23)	(2.60)	(8.16)	
1980	271	−78677.5	108.96	0.42	93.75	0.02	2527.30	−4.51	—	9517.2	463.3	1655	−2447	0.89
		(2.22)	(1.52)	(0.57)	(1.45)	(1.33)	(2.09)	(1.49)		(1.94)	(1.87)	(1.44)	(9.25)	
1981	137	−18958.9	−1549.55	5.65	74.99	0.08	3105.60	−1.03	—	3959.1	28.6	12949	−3527	0.78
		(1.25)	(2.28)	(2.09)	(1.60)	(1.65)	(2.06)	(0.05)		(1.87)	(1.39)	(1.74)	(7.20)	

[1]Variables are defined as follows: 1) GRT and GRT² are gross registered tonnage and its value squared; 2) HPWR and HPWR² are engine horsepower and its value squared; 3) LN and LN² are vessel length and its value squared; 4) YEAR is the year of observation; 5) DNO is a dummy variable for new and used vessels (1 = new, 0 = otherwise); 6) FI is a nonbinary dummy variable for gear type; 7) CS is a dummy variable for hull construction (1 = steel, 0 = otherwise); and 8) AGE is the age of the vessel.

[2]Numbers in parentheses are t-statistics.

Atlantic Fisheries and increased fuel prices between 1972 and 1975; 3) the formulation and implementation of the Fisheries Conservation and Management Act in 1976 and 1977; 4) extremely restrictive regulations in 1978 and 1979; and 5) a long dock strike in New Bedford, frozen harbors, and foreign purchases from American fishermen in 1981. In addition, there was substantial entry of new steel-hulled vessels between 1975 and 1977 and 1979 and 1980.

Chow (1960) tests of the equality of regression equations were conducted to further examine the possibility that the statistical relationships between cost and vessel characteristics changed over time. The Chow test is an F-test of the stability of the coefficients (Maddala 1977). The results of these tests are presented in Table 3.

The results of the tests indicate that the estimated relationships between cost and characteristics were not the same for the selected time periods. Alternatively, the hypothesis of the equality of the regression equations for different periods of time could not be accepted at any reasonable level of significance. However, these results only verify that different models should be estimated for different periods of time. They are not conclusive proof of the selection of the years for a particular group of years. A more accurate determination of the years to be included in each group requires considerably more estimation and hypothesis testing which is beyond the intent of this study.

As indicated by the t-statistics in Tables 1 and 2, the age of the vessel, whether or not the vessel is new or used, and the size characteristics appear to be the more statistically significant explanatory variables. These results are consistent with the results of Griffin et al. (1978). The statistically significant negative coefficients for the size characteristics during the years 1972–75 are particularly interesting. These years coincide with the Arab oil embargo when fuel prices increased; expected increases in future operational costs may have deterred new entry. The results also indicate that the value of a vessel declines as it becomes older. The coefficient for hull construction, CS, suggest that steel-hulled vessels are more expensive than are those of other materials such as fiberglass, ferro cement, wood, and aluminum. There does not appear to be a difference in the value of a vessel based on gear type. This may be a result of specification problems with the dummy variable for gear type (see footnote 7).

It is of further interest to examine the elasticities of cost with respect to the vessel characteristics.[10] These are presented in Table 4. As indicated, vessel tonnage, length, and age have the greatest influence on the acquisition price. The elasticity for length is consistent with the manner in which vessels are sold; that is, vessel prices are largely stated in terms of their length.

There are, however, inconsistences in the estimated capital stock equations and elasticities. In

TABLE 3.—Results of tests for the equality of regression equations.

Periods tested	F-statistic[2]	Critical values[1] 0.05	0.01
1965–71 1972–75 1976–77 1978–79 1980–81	39.38	$F_{12,1050} = 1.75$	$F_{12,1050} = 2.18$
1965–71 1972–75	8.45	$F_{12,325} = 1.75$	$F_{12,325} = 2.18$
1965–75 1976–81	20.55	$F_{12,1086} = 1.75$	$F_{12,1086} = 2.18$
1965–75 1976–79	21.33	$F_{12,668} = 1.75$	$F_{12,668} = 2.18$
1976–77 1978–79	3.60	$F_{12,329} = 1.75$	$F_{12,329} = 2.18$
1976–77 1978–81	3.22	$F_{12,737} = 1.75$	$F_{12,737} = 2.18$
1976–79 1980–81	3.35	$F_{12,737} = 1.75$	$F_{12,737} = 2.18$
1980 [3]1981	2.76	$F_{12,384} = 1.75$	$F_{12,384} = 2.18$

[1]F-statistic for denominator degrees of freedom equal to infinity.

[2]Restricted residual sum of squares obtained by pooling data over all time periods and estimating Equation (2). Unrestricted residual sum of squares obtained by estimating Equation (2) for each period being examined and then adding the residual sum of squares for each equation.

[3]Residual sum of squares obtained from estimating Equation (2) without the time variable.

[10] Elasticities indicate the percentage change in cost resulting from a 1% change in the value of a characteristic.

TABLE 4.—Estimated elasticities of cost with respect to vessel characteristics.[1]

Year	Elasticities GRT[2]	HPWR	LN	AGE
1965–71	0.43	0.06	2.88	−0.32
1972–75	0.78	−0.04	−0.08	−0.08
1976–77	1.14	0.09	0.11	−0.11
1978–79	−0.14	0.30	2.38	−0.40
1980	0.16	0.30	1.43	−0.30
1981	−0.64	0.56	2.38	−0.41

[1]Elasticities based on nominal estimates and observed mean values of cost and vessel characteristics.

[2]GRT is gross registered tonnage; HPWR is engine horsepower; LN is length; AGE is age of vessel.

particular, not all of the estimated coefficiencts have the desired or expected sign. For example, the coefficient for tonnage in the 1981 estimate is negative and that for the square of tonnage is positive. In contrast, a positive coefficient for tonnage was expected since vessel cost should increase with vessel tonnage, and the coefficient for tonnage squared was expected to be negative because vessel costs are believed to increase at a decreasing rate.

The incorrect signs could be the result of multicollinearity between vessel characteristics. Auxiliary regressions, though, do not indicate severe multicollinearity. The R^2 values are <0.35. If multicollinearity is a problem, its major effect is on the estimated relationships between cost and individual characteristics, the estimated elasticities, and the previously discussed Chow tests.

Multicollinearity is not thought to be a problem for several reasons. First, Chow tests in the presence of multicollinearity usually result in the acceptance of the null hypothesis of the equality of regression equations or that differences in the estimated coefficients are statistically insignificant (Maddala 1977). Second, multicollinearity does not pose a problem for estimating capital stock and investment; the estimated equations still permit estimation of the conditional mean.[11]

[11] For additional information on the problems of multicollinearity with respect to analysis and prediction, see Kmenta (1971).

The equations for the real or deflated value of capital were used to estimate total capital stock and investment for the New England fleet between 1965 and 1981. The real capital stock equations were applied to vessel data available from the Northeast Fisheries Center, and total capital stock was calculated as the sum of the stock over all vessels. Aggregate net investment was calculated as the difference in total capital stock between consecutive years.

Prior to estimating total capital stock and investment, it was necessary to define vessel type by gear to avoid double counting which might occur since vessels frequently switch port and gear. Three categories of gear types were established: 1) otter trawl, 2) scallop dredge, and 3) all others, which include lobster trawl and pots, herring gear, harpoons, etc. Vessels were assigned a gear type based on a plurality of days at sea. Estimates of capital stock and investment are presented in Table 5.

Several limitations should be considered when evaluating the estimates. First, there is the previously discussed problem that estimates of capital stock may be biased or overestimated. Second, estimates are only for New England vessels or those which are believed to be homeported in New England. Third, the capital stock and investment series pertain to New England and not the United States; that is, estimates should not be interpreted as net changes in the capital stock and investment in U.S. fisheries. Fourth, under-

TABLE 5.—Estimates of real capital stock and investment in New England harvesting sector, 1965–81.[1]

Year	Number of vessels	Capital stock			Investment			Index of investment
		Trawl	Dredge	Other	Trawl	Dredge	Other	
		$ Millions						
1965	594	25.96	16.29	1.98				
1966	619	28.84	14.75	2.82	2.88	−1.54	0.84	100
1967	628	39.37	11.42	1.63	10.53	−3.33	−1.19	276
1968	610	28.65	15.43	1.68	−10.72	4.01	0.05	−301
1969	602	29.22	12.92	1.29	0.57	−2.51	−0.39	−107
1970	607	25.61	8.29	1.37	−3.61	−4.63	0.08	−374
1971	620	23.65	12.80	1.47	−1.96	4.51	0.10	122
1972	655	27.01	7.74	4.70	3.36	−5.06	3.23	70
1973	666	28.42	7.12	5.13	1.42	−0.62	0.43	56
1974	695	21.26	4.19	6.40	−7.17	−2.93	1.27	−405
1975	737	29.04	5.15	8.48	7.78	0.96	2.08	496
1976	783	20.73	7.72	8.16	−8.31	2.57	−0.32	−278
1977	836	28.86	14.19	7.86	8.13	6.47	−0.30	656
1978	881	37.45	12.85	8.65	8.59	−1.34	0.79	369
1979	1,107	45.41	27.30	11.25	7.96	14.45	2.60	1147
1980	1,260	52.26	34.30	11.69	6.85	7.00	0.44	656
1981	1,246	43.35	30.15	11.60	−8.91	−4.15	−.09	−603

[1]Real investment and capital are deflated with producer price index for heavy machinery, 1967 = 100.

tonnage vessels or those which are <5 gross registered tons are excluded since data are unavailable; thus, total capital stock and investment in New England fisheries are underestimated.

Despite these limitations, the results provide information on investment and capital stock in New England fisheries which has not been available. As is characteristic of open-access fisheries, investment in New England fisheries appears to have increased over time. This is quite evident subsequent to the passage of the Magnuson Fisheries Conservation and Management Act of 1976. While possibly true, the observation that investment increased when the act was passed should not be construed to imply that the act was responsible for increased investment. Positive expectations regarding fish stocks or economic conditions could also be responsible for increases in capital stock and investment.

The largest increase in investment occurred in 1979 which coincided with the greatest influx of vessels. It also coincided with increased fish stocks in 1978 and 1979 and high vessel profits of the previous year. In 1979, 226 vessels entered the New England fisheries; 92 vessels were newly constructed.

Disinvestment also occurred, but the reasons are unknown.[12] Disinvestment may be associated with vessel sinkings, foreclosures on vessel mortgages, and exit from the region. Alternatively, if vessel prices reflect the expected net discounted present value of earnings from a fishery, the disinvestment or even changes in investment may be due to changes in economic expectations. Disinvestment occurred between 1968 and 1970, 1974, 1976, and in 1981.

Disinvestment between 1968 and 1970 may reflect expectations of declining future earnings. Disinvestment in 1974 may reflect the effects of high fuel prices. Disinvestment in 1976 and 1981 may be associated with fishermen's expectations of declining fish stocks, the effects of management, and high fuel prices.

The reasons for investment are also unknown. Increasing levels of investment between 1977 and 1980 may be due to economic expectations associated with fisheries management, fish stocks, and future earnings.

The real capital stock increased approximately 6% per year between 1965 and 1981. The largest increase occurred in 1978 and 1979 when there was a substantial increase in the number of new steel-hulled vessels and entry of vessels from the mid-Atlantic region. Capital stock declined in 1981 when some of the mid-Atlantic vessels left New England and the stocks of fish, particularly sea scallops, declined (Northeast Fisheries Center 1985).

The results also indicate why a vessel count should not be used to indicate capital stock or investment. The number of vessels increased between 1969 and 1970 and 1975 and 1976, but investment decreased in 1970 and 1976 (Table 6). Alternatively, the number of vessels increased in each year relative to 1965, but the real capital stock between 1969 and 1976 declined with respect to 1965.

TABLE 6.—Indices of capital stock based on constant dollar value and vessel count.

	Capital stock					
	Constant dollar value			Vessel count		
Year	Trawler[1]	Dredge[1]	Total	Trawler[1]	Dredge[1]	Total
1965	100	100	100	100	100	100
1966	111	91	105	102	94	104
1967	152	70	119	109	77	106
1968	110	95	103	104	106	103
1969	113	79	98	104	106	101
1970	99	51	80	108	74	102
1971	91	79	86	108	83	104
1972	104	48	89	108	74	110
1973	109	44	92	105	79	112
1974	82	26	72	107	49	117
1975	112	32	96	105	66	124
1976	80	47	83	109	202	132
1977	111	87	115	107	202	141
1978	144	79	133	116	189	148
1979	175	168	190	137	313	186
1980	201	211	222	158	440	212
1981	167	185	192	158	413	210

[1]Gear type assigned by plurality of days absent.

The inadequacy of using vessel count is more pronounced when comparing the indices based on gear type. As shown in Table 6, the number of trawl vessels in every year exceeded the number of vessels in 1965 while capital stock was less than that of 1965 for four years. The two scallop dredge indices also indicate dissimilar changes between vessel count and real capital stock. It may, though, be possible than an index based on vessel count and weighted by vessel size would more closely compare to the real capital stock index. The construction of these indices would require considerable additional analysis and determination of the weights necessary for aggregation.

[12]Hirshleifer (1970) provided additional information about disinvestment.

SUMMARY AND CONCLUSIONS

This study developed procedures for estimating the capital stock and net investment using only the information generally available. That is, data on acquisition and list prices for some but not all vessels and characteristics for most vessels in a fleet were used to estimate capital stock and investment in a fishery. An hedonic approach which specified the acquisition price as a function of vessel characteristics was suggested as a possible method for obtaining information necessary for estimating capital stock and net investment. It was argued that the approach was consistent with procedures used by economists to estimate the capital stock and investment in traditional industries.

Estimates were based on 1,110 observations obtained from NMFS and classified advertisements for the period 1965–81. Vessel characteristics pertaining to size and age were shown to be the more significant characteristics for explaining the value of a vessel. The corresponding information was then used to estimate the capital stock and investment in the New England fisheries.

An interesting result was that although investment increased over time, there also was disinvestment in the fisheries. It was suggested that this was possibly the result of vessel sinkings, exit of vessels from the region, foreclosures, and expectations of declining future net returns.

It also was demonstrated that a vessel count should not be used to indicate capital stock or investment. The number of vessels generally increased over time, but the level of capital stock did not coincide with these changes. This suggests that more attention should be given to developing economic measures of capital stock and investment.

A question still in need of attention, however, cannot be answered from this study. That is, given the level of investment, can an optimal utilization and allocation of resources be determined. The answer is clearly no. This requires management authorities to specify the objectives of fisheries management and a detailed bioeconomic model.

There is a need for more research on investment, and in particular, the determination of the optimum rate of investment. This includes research on the social discount rate, reasons for investment, and the marginal productivity of capital. More important, additional research is required to better address the issues of fisheries management, particularly whether or not public expenditures should be allocated to managing fisheries.

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A COMPREHENSIVE THEORY ON THE ETIOLOGY OF BURNT TUNA

CHERYL WATSON,[1] ROBERT E. BOURKE,[2] AND RICHARD W. BRILL[3]

ABSTRACT

Over the past 14 years, the Hawaii handline fishery has experienced phenomenal growth in the catch for large yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *Thunnus obesus*. These fish are primarily caught for the sashimi (raw consumption) market but have been continually plagued with a product quality problem known as "burnt tuna" or, in Japanese, yake niku. Not only does this problem significantly reduce the value of the catch, it also limits export markets and expansion of this low-capital, high-return fishery to other areas of the Pacific. Previous research and suggestions for mitigating burnt tuna have centered on the hypothesis that it is caused by high muscle temperature and low pH, which is the result of a violent struggle during capture.

A new, more comprehensive hypothesis is presented: Burnt tuna is actually caused by the postmortem activation of enzymes known as calcium-activated proteases and by the enhancement of the effect of these enzymes by high blood catecholamine levels. Previously unexplainable observations, such as the propensity of female fish to become burnt more often during the summer months, the efficacy of brain destruction in preventing burnt tuna, and the lack of effect of cooling on the incidence of burnt tuna, are explainable in light of this new hypothesis.

One of the largest fisheries in Hawaii is the handline fishery for large (>50 kg) yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, caught primarily for raw consumption as sashimi. Yearly landings increased from 89 short tons (ex-vessel value, $131,000) in 1973 to 615 short tons (ex-vessel value, $2.1 million) in 1984 (Yuen 1979; Hudgins and Pooley 1987). The total economic value of the fishery has been estimated as high as $5 million yearly (Ikehara[4]). In Hawaii, the night handline fishery is known as ika shibi from the Japanese words for squid and tuna, and the daytime fishery is known as palu ahi from the Hawaiian words for chum and yellowfin tuna. There is also growing international interest in this type of fishing because of its low initial capital investment, low operating and fixed expenses, strong export markets, and high profitability (Strong 1979; Gibson 1981; Jerrett 1984). Boats can be as small as 6 m and require only one- or two-man crew. Catch rates in Hawaii have ranged from two fish per hook per night (Yuen 1979) to one-half fish per hook per night (Bourke[5]), illustrating the profitability for the individual fisherman.

Unfortunately, handline (as well as primarily recreational trolling) fishermen are plagued by a product quality problem known as "burnt tuna" or, in Japanese, as yake niku (literally translated as "cooked meat"). When fish are intended for raw consumption, product quality is of utmost importance. Prime quality tuna flesh should be red, translucent, and firm and have a delicate flavor. Burnt tuna is pale, exudes a clear fluid, and has a soft texture and a slightly sour taste. Although perfectly palatable when cooked or canned, burnt tuna is considered unsuitable for raw consumption and commands only a fraction of the price of prime quality fish. Fish are usually exported whole to preserve freshness, so burnt tuna often is not detected until shipping costs have been incurred. This discourages exports of tuna caught from areas or via fishing techniques with high incidences of the problem.

Burnt tuna affects from 5 to 100% of the tissue from an individual fish and ranges from mild to severe. Approximately 25% of the fish caught by the Hawaii handline fishery are burnt, as are 50% of the large yellowfin tuna caught by commercial and recreational trollers (Bourke fn. 5).

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[4]Ikehara, W. N. 1981. A survey of the ika-shibi fishery in the State of Hawaii, 1980. Southwest Fish. Cent. Adm. Rep. H-82-4C, 12 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.

[5]Bourke, R. E. 1985. Hilo ikashibi fishery 1984 survey: Problems of a maturing fishery and a potential solution to the burnt tuna problem. Poster presentation at 1985 Tuna Conference.

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Annual losses to the handline fishery are an estimated 16% of the value of the total catch (Cramer et al. 1981). The problem has also been reported in fish intended for raw consumption caught by purse seine (Nakamura et al. 1977). Surprisingly, the problem rarely occurs in fish caught by longlining (Williams 1986).

PAST RESEARCH ON BURNT TUNA

The Japanese were the first to investigate the causes of burnt tuna and possible mitigating strategies (Itokawa 1968, 1969). The first controlled laboratory investigations were those of Nakamura et al. (1977) and Konagaya and Konagaya (1978, 1979). Nakamura et al. (1977) concluded that high muscle temperature and low muscle pH caused myofibrillar protein denaturation and also noticed that, once denaturation began, it continued even if the tissue was kept at 0°C. Because of the relatively high thermostability of tuna myofibrillar protein and because yake niku occurs in species (e.g., frigate mackerel and sardine) that do not generate high muscle temperatures during struggling, Konagaya and Konagaya (1978) concluded that acid denaturation of myofibrillar proteins at moderate temperatures was the underlying cause.

Cramer et al. (1981) studied handline-caught yellowfin tuna in Hawaii and found that the occurrence of burnt tuna did not correlate with muscle temperature at time of landing and correlated only loosely with extracellular muscle pH. Ikehara[6] conducted an engineering study to develop methods to cool large yellowfin tuna more rapidly, the presumption being that rapid cooling would prevent muscle degradation. Although successful in developing a technique to increase cooling of deep muscle temperature, as shown in Figure 1, there was no apparent correlation between rate of cooling and incidence of burnt flesh. In spite of this lack of directly observed correlation, some publications designed for fishermen still stress that high muscle temperatures and low muscle pH are the prime causes of burnt tuna (Gibson 1981). Others have expressed doubt as to the validity of this hypothesis (Jerrett 1984).

The high muscle temperature-low pH hypothesis appears to fit with what is known about tuna physiology, in that these fishes are capable of producing muscle temperatures significantly above ambient (Carey et al. 1971; Carey 1973) and exhibit some of the highest rates of muscle glycolysis (production of muscle lactate and concomitant production of acidity) observed in nature (Hochachka et al. 1978; Hochachka and Mommsen 1983). Yet some observations do not fit this hypothesis. For example, burnt tuna occurs more frequently in summer, more frequently in female fish, and more frequently in fish fought for short periods of time than in fish fought for long periods (>7 minutes or <2 hours) (Davie and Sparksman 1986; Nakamura[7]). Furthermore, burnt tuna occurs rarely in longline-caught fish and in fish subjected to brain or spinal column destruction immediately following capture (Nakamura et al. 1977; [Suisan Sekai] 1977; Cramer et al. 1981; Davie and Sparksman 1986; Nakamura fn. 7). The hypothesis that burnt tuna is caused by high muscle temperature and low muscle pH does not seem to directly fit with any of these observations.

A NEW ANALYSIS OF THE BURNT TUNA PROBLEM

At the biochemical level, the high muscle temperature-low pH hypothesis would predict that the observed drop in extracellular pH would be accompanied by a similar drop in intracellular pH and activation of lysosomal proteases. These proteases would then degrade actin and myosin, the dominant muscular proteins, resulting in the

[6]Ikehara, W. N. 1981. Development of a small-boat chilling system for the reduction of burnt tuna. Final Report for a Pacific Tuna Development Foundation contract, var. pag.

[7]R. Nakamura, Department of Animal Sciences, University of Hawaii, Honolulu, HI 96822, pers. commun. October 1987.

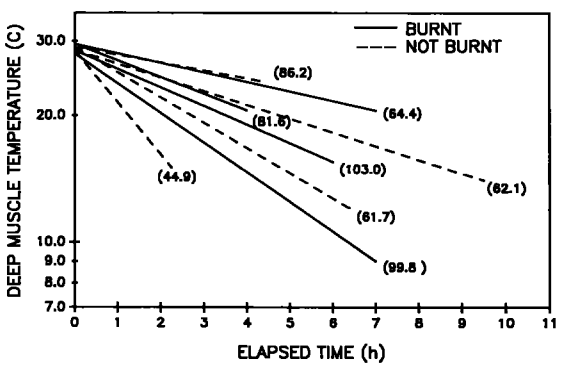

FIGURE 1.—Data are from Ikehara (text fn. 6). Initial and final deep muscle temperatures are plotted on semilogarithmic axes to linearize the rate of temperature change. Numbers in parentheses are the body weight (kg) for each fish.

undesirable changes seen in burnt tuna. The lysosomal proteases, specifically cathepsins B, D, and L, have an optimum pH of about 5 (Dahlmann et al. 1984). However, recent work by Abe et al. (1985, 1986) has shown that, intracellularly, tuna muscle is well buffered and that a fall in extracellular pH is not necessarily accompanied by an equivalent fall in intracellular pH. Using ischemic rat gastrocnemius muscle, Hagberg (1985) found that a 1 pH unit drop (7.30–6.36) in extracellular pH was accompanied by a drop in intracellular pH of only 0.4 unit (7.00–6.60). Thus, the acidic intracellular environment that would favor the action of the lysosomal proteases probably is not present in burnt tuna. Also, with the exception of calcium-activated neutral protease, all other muscle proteases (cathepsins B, D, L; alkaline serine protease; neutral trypsin-like protease; and alkaline cysteinyl protease) degrade myosin (Dahlmann et al. 1984). Yet Hochachka and Brill (1987) found burnt muscle had no increase in 3-methyl-histidine, a specific marker for myosin breakdown. Decomposition of other myofibrillar proteins is, therefore, implicated.

Electronmicrographs of postmortem burnt tuna muscle (Davie and Sparksman 1986) showed a consistent, rapid disintegration of Z-discs and irregularities in the sarcoplasmic reticulum (SR). The changes in burnt muscle were not different in kind from postmortem changes seen in unburnt tissue, but were a result of a significant increase in the rate of disintegration. Selected destruction of the Z-discs, troponin and tropomyosin, and the SR is characteristic of a pair of proteases known as calcium-activated neutral proteases (CANP's) (Sugita et al. 1984; Suzuki et al. 1984). These proteases are cytoplasmic, ubiquitous, activated by increased intracellular calcium levels, and active at pH 5.5–8.0 (Sakamoto and Seki 1985; Koohmaraie et al. 1986; Seki and Kimura 1986; Zeece et al. 1986b). The intracellular pH most likely found in burnt tuna muscle is, therefore, more consistent with CANP action than with lysosomal proteases whose activity requires a pH closer to 4.5 (Hochachka and Brill 1987). In addition, while cathepsin D's activity is greatly restricted at 15°C, CANP is still active at 5°C (Koohmaraie et al. 1986; Zeece et al. 1986a).

A new etiology of burnt tuna proposed by Hochachka and Brill (1987) is summarized in Figure 2. Their hypothesis predicts that low intracellular ATP concentrations lead to the leaking of Ca^{++} into the cell and increases in intracellular

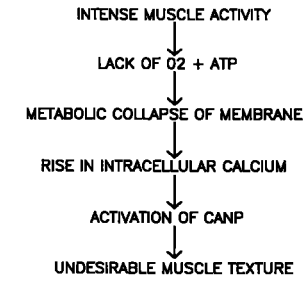

FIGURE 2.—Biochemical reactions involved in the development of burnt tuna as proposed by Hochachka and Brill (1987).

Ca^{++} concentrations. These increases, in turn, activate CANP, which specifically attacks troponin, tropomyosin, SR, and mitochondria. The breakdown of the latter two intracellular organelles releases more calcium into the cytoplasm, thus further increasing the activity of CANP.

The effect of brain and spinal cord destruction on reducing the incidence of burnt tuna and of similar muscle degradation seen in other fish species can be explained by this new hypothesis, which assumes the initial drop in ATP is the root cause of the elevated intracellular calcium (Amano et al. 1953; Fujimaki and Kojo 1953; Konagaya and Konagaya 1978; Ikehara fn. 6). Brain destruction maintains elevated muscle ATP levels after capture (Boyd et al. 1984). Data recently collected on the use of brain and spinal cord destruction in large yellowfin tuna (Fig. 3)

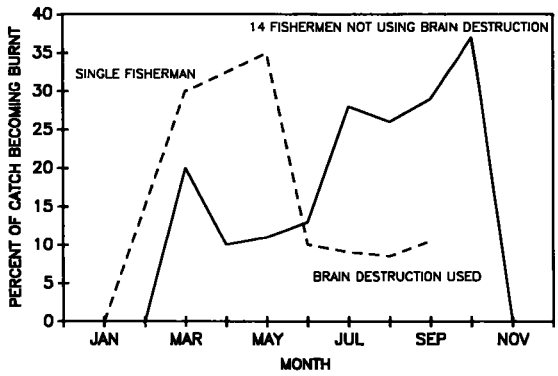

FIGURE 3.—Incidence of burnt tuna occurring in large yellowfin tuna caught by 14 commercial handline fishermen operating out of Hilo, HI, January–September 1984, and by 1 fisherman who began using brain destruction in May. His incidence of fish becoming burnt dropped dramatically in spite of the normal summer increased incidence seen in the catch of 14 other fishermen.

clearly show the effectiveness of this technique in preventing burnt tuna. A drop from 30 to <10% of the tuna becoming burnt was noted when the fisherman changed his killing technique from shooting to the use of a brain spike.

A MORE COMPREHENSIVE HYPOTHESIS ON THE ETIOLOGY OF BURNT TUNA

The hypothesis presented by Hochachka and Brill (1987) does not explain all the observed factors leading to tunas' different propensity to become burnt. It cannot explain why tunas struggling for <7 minutes rarely become burnt (Nakamura fn. 7), nor can it account for the observations of Davie and Sparksman (1986) and Bourke (unpubl. data), who found that tuna struggling for extended (>1 hour) periods of time have a lower probability of becoming burnt. It also cannot explain why female fish become burnt more often than males (Nakamura et al. 1977), or why fish caught in summer become burnt more often (Fig. 3).

Our revised hypothesis is presented in Figure 4. We have incorporated into the Hochachka and Brill (1987) hypothesis, the action of the neurotransmitters-hormones norepinephrine (NE) and epinephrine (E) (collectively referred to as catecholamines). Periods of intense physical activity or capture stress increase the levels of circulating catecholamines by about 10–200 times in fish other than tunas (Nakano and Tomlinson 1967; Ling and Wells 1985). Most likely a similar situation occurs in tuna during hooking, fighting, and capture. The importance of elevated circulating catecholamines in this particular schema comes from their potentiating effect on the action of CANP. Catecholamines cause the phosphorylation of troponin, resulting in a more rapid and prolonged proteolysis of this muscle structure (Toyo-oka 1982); in other words, high circulating levels of catecholamines greatly increase the effectiveness of the enzymes responsible for a tuna becoming burnt.[8]

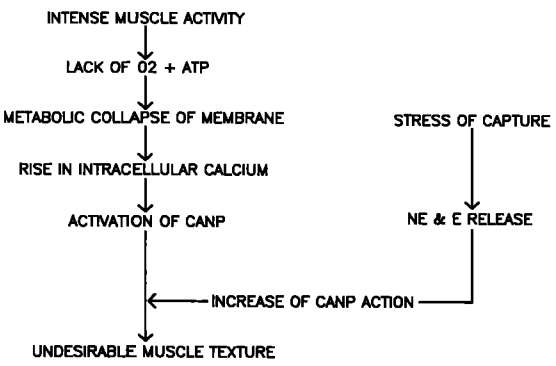

FIGURE 4.—Comprehensive theory of the etiology of burnt tuna proposed in this paper.

The gills are the organ primarily responsible for the degradation of catecholamines, and circulating catecholamines are rapidly cleared from the blood (Nekvasil and Olson 1986). We estimate circulating catecholamines in tuna have a half-life of 30 minutes or less. Therefore, we hypothesize that, in a longline-caught fish remaining in the water for several hours after hooking (Davie and Sparksman 1986), plasma catecholamines are reduced to low levels before the fish is landed and killed, thus resulting in a low percentage of burnt fish. Similarly, fish caught by rod and reel or by handline and fought for several hours would have the low circulating catecholamine levels and low propensity to become burnt. Indeed, Gibson (1981) recommends that handline-caught fish be attached to a buoy and left for an hour prior to being brought on board and killed, as a measure to prevent burnt tuna. That this technique presumably lowers blood catecholamine levels prior to death could explain its efficacy. On the other hand, we hypothesize that a fish landed during the peak of its blood catecholamine concentrations would have the greatest propensity for becoming burnt. This indeed appears to be the case.

The mechanism that ties catecholamines to the observed seasonality and increased number of female fish becoming burnt lies in the biochemical structural similarity of catecholamines and reproductive steroids, particularly estrogen. These steroids reach a peak during spawning season, which is May through October for yellowfin tuna in Hawaii (June 1960). A corresponding increase occurs in the percentage of the tuna catch that becomes burnt during this season (Fig. 3). In the presence of tyrosine hydroxylase, estrogen is converted to catecholestrogen and consequently competes for the same degradative enzymes in the gills, therefore slowing the clearance of catecholamines from the blood (Nekvasil and Olson 1986). Female fish, with high circulating estrogen levels, would then be expected either to reach

[8]Although cortisol is also known to be released during stress, its mechanism of action is much slower than NE or E, making it unlikely that it could exert catabolic effects within 15 minutes.

higher maximum circulating catecholamine levels or to maintain high levels for longer periods, thus explaining the greater number of female fish that become burnt and the seasonality of the occurrence of burnt tuna.

As pointed out by Davie and Sparksman (1986) and Hochachka and Brill (1987), burnt tuna is a quantitative change in tissue decomposition, not a qualitative one. High blood catecholamine levels at the time of death act as accelerators in this inevitable metabolic cascade. However, because we are dealing with a change in rate, the action of catalysts can make all the difference as to whether or not a fish becomes burnt due to CANP.

FUTURE RESEARCH

Under normal conditions, CANP is inhibited by calpastatins. This class of proteins is distinct from the other cysteine protease inhibitors, the cystatins. Although the cystatins can inhibit cathepsins B and H, they are unable to alter CANP activity. Conversely, calpastatin is only effective against calcium-activated neutral protease (Barrett et al. 1986; Parkes 1986). Unfortunately, almost nothing else is known about the relationship of CANP to its endogenous inhibitor, either structurally or physiologically. Certainly investigations into the role of calpastatin would prove valuable for this research.

Immediate future research will concentrate on tracking the specific action of CANP in burnt tuna and attempting to stop this action with Ca^{++} chelating agents such as EGTA (ethyleneglycol-bis-(aminoethyl ether)-N,N,N′,N′-tetraacetic acid) or by use of its intracellular inhibitor, calpastatin. Also, blood catecholamine levels of stressed and unstressed fish will be measured, along with metabolic clearance rates of norepinephrine and epinephrine.

When viewed as a process of metabolic deregulation of CANP, the rapid deterioration of tuna muscle ceases to be an isolated muscular phenomenon. The Z-disc disintegration characteristic of burnt tuna is also present in cardiac muscle injury due to ischemia and muscular dystrophy (Sugita et al. 1984). Given the highly conserved nature of muscle tissue, an understanding of burnt tuna may also provide insights into the metabolic processes of human disease.

ACKNOWLEDGMENTS

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REPRODUCTIVE BIOLOGY OF THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*, IN SOUTH TEXAS[1]

NANCY BROWN-PETERSON,[2] PETER THOMAS,[3] AND CONNIE R. ARNOLD[3]

ABSTRACT

The spotted seatrout, *Cynoscion nebulosus*, spawns from April through the end of September in shallow bays in South Texas. All females were sexually mature at 300 mm SL and males at 200 mm SL. Histological examination of the testes showed that spermatogenesis began in January and continued until September, although spermatozoa remained in the testes until November. Spermatogenesis was more active in the peripheral lobules of the testes than in the central lobules during the latter half of the spawning season. The sequence and timing of final oocyte maturation (FOM) was investigated for the first time in this species. Lipid coalescence began at dawn and germinal vesicle migration started by midmorning. By early afternoon, oocytes were hydrated and spawning occurred at dusk.

Evidence of multiple spawning was examined. Morphological and histological data showed that oocytes were continually recruited from March through the end of September, and the percentages of vitellogenic and fully yolked oocytes did not decline during the spawning season. An average of only 15.5% of the vitellogenic oocytes underwent FOM and hydration during a single spawn. Postovulatory follicles were found in many fish with mature ovaries throughout the reproductive season. Laboratory studies showed that this species is capable of repeated spawns. Batch fecundity was best predicted by ovary-free body weight of the fish and averaged 451 ± 43 eggs/g ovary-free body weight. Estimates of spawning frequency ranged from every other day to once every three weeks.

The spotted seatrout, *Cynoscion nebulosus*, supports important commercial and recreational fisheries throughout its range (Chesapeake Bay, Virginia to Tampico, Mexico; Tabb 1966). Whereas aspects of the reproductive biology of this sciaenid species have been documented throughout its range (i.e., Chesapeake Bay: Brown 1981; Georgia: Mahood 1975; Florida: Moody 1950, Klima and Tabb 1959, Tabb 1961; Mississippi: Overstreet 1983; Louisiana: Hein and Shepard 1979; Texas: Pearson 1929, Miles 1950, 1951), a comprehensive study of reproduction in spotted seatrout does not exist for any area. An extensive knowledge of the reproductive life history of a species is necessary to understand certain aspects of its reproductive physiology and endocrinology. Most previous studies have concentrated on the size at sexual maturity and the extended spawning season of this species (Pearson 1929; Moody 1950; Tabb 1961; Mahood 1975). A protracted spawning season is generally characteristic of multiple spawners (Nikolskii 1969). In addition, Overstreet's (1983) histological data suggest that *C. nebulosus* may be a multiple spawner. However, the possibility that spotted seatrout are multiple spawners has not been thoroughly discussed in the literature, and previous estimates of fecundity (Sundararaj and Suttkus 1962; Overstreet 1983) have not considered the multiple spawning nature of *C. nebulosus* or have included estimates of batch fecundity.

In the present study, the reproductive biology of *C. nebulosus* in South Texas was investigated, and particular attention was given to evidence for multiple spawning and estimates of batch fecundity and spawning frequency. The spawning season, spawning sites, time of spawning, and percentage of running ripe fish were documented. In addition, the temporal pattern of final oocyte maturation was determined. The histological appearance of the gonads was examined, and particular attention was given to the presence of postovulatory follicles in ovarian tissue, an indicator of multiple spawning in the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980). The size-frequency distribution of vitellogenic oocytes was examined, since this can indicate multiple spawning (deVlaming 1983). Batch fecundity was determined and spawning frequency

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was estimated from both field-caught and laboratory fish.

MATERIALS AND METHODS

Collection of Samples

Spotted seatrout were collected in Redfish Bay or Lydia Ann Channel near Port Aransas, TX, U.S.A. at depths of 1–3 m (Fig. 1). Fish were captured using a 300 m gill net (82 mm stretch) or a 300 m trammel net (outer panels, 178 mm stretch; inner panel, 89 mm stretch) over shallow beds of turtle grass, *Thalassia testudinum* or shoal grass, *Halodule wrightii*, bordered by a 1–2 m drop-off into a channel. Fish <300 mm SL were captured with hook and line in 1–2 m of water.

Samples were collected weekly or twice monthly from March 1982 through early May 1985. No samples were taken in November and December 1983, October and December 1984, and February 1985. During 1982, samples were collected at dusk only; in 1983, 1984, and 1985, samples from dawn, midday, and midnight were also taken. During each sampling period, salinity and temperature were recorded as well as the time of capture.

Analysis of Fish and Gonads

Total length (TL) and standard length (SL) were measured to the nearest mm for each specimen and total body weight (WT) was determined to the nearest 10 g. Gonads were removed and weighed to the nearest 0.1 g (gonad weight, GW) and the gonadosomatic index (GSI) was calculated, using the formula: GSI = (GW/WT) × 100.

Reproductive stage of the gonads was assessed macroscopically using the criteria in Table 1. The macroscopic criteria used were similar to those used by Overstreet (1983) and Macer (1974). A small portion of tissue was removed from the anterior or midsection of one gonad from each fish and preserved in Davidson's fixative for histological analysis (Jones 1966). Tissues were dehydrated and embedded in paraffin. Seven micron sections were cut and stained with Harris' hematoxylin and counterstained with eosin. Reproductive stage of each sample was assessed microscopically using the criteria in Table 1. Fish with

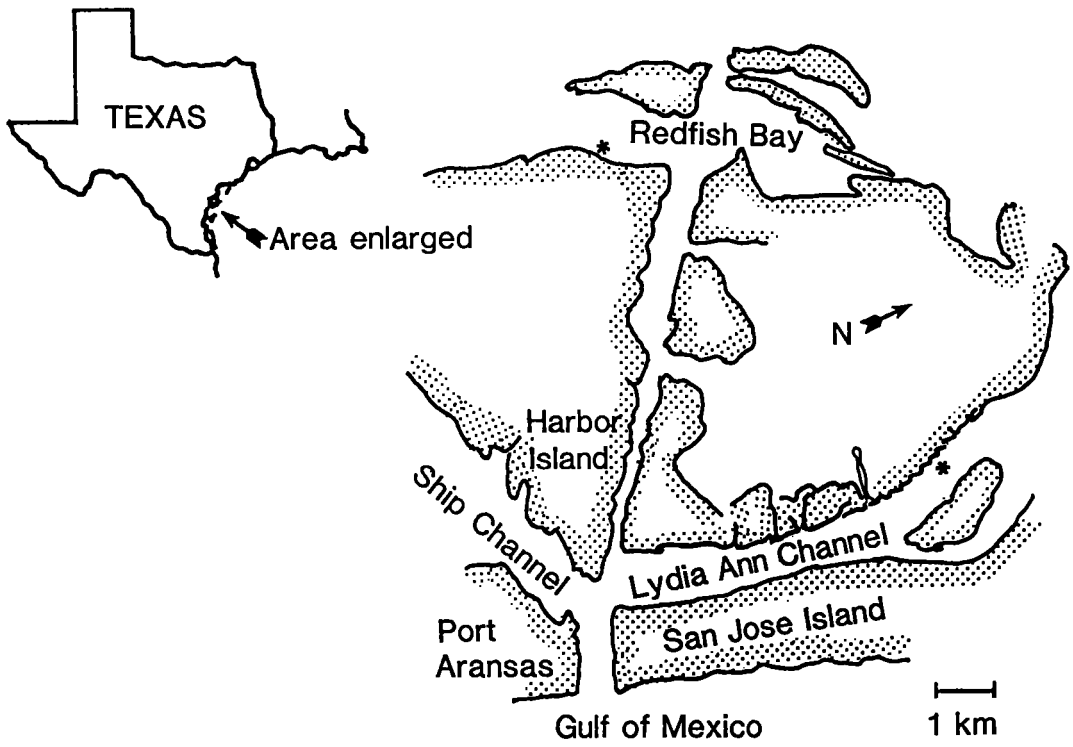

FIGURE 1.—Location of spotted seatrout sampling sites in South Texas. Asterisks denote sampling sites.

mature gonads were considered sexually mature. The microscopic criteria used were similar to those described by Yamamoto (1956), Hyder (1969), and Macer (1974). The percentages of each stage of oocyte, atretic structures, and postovulatory follicles were determined from histological slides of the ovaries of females >305 mm SL by counting all the oocytes in three randomly selected fields of view. An oocyte was counted if >50% of the cell was in the field of view. Two hundred and fifty to 500 oocytes were counted for each histological specimen.

A small portion of tissue (<0.5 g) was removed from the center of each ovary of females >305 mm SL collected in 1984 and 1985, placed in clearing solution (6 parts ethanol, 3 parts formalin, 1 part

TABLE 1.—Criteria used to describe gonadal reproductive stages of male and female spotted seatrout collected in South Texas.

Stage	Sex	Macroscopic appearance	Microscopic appearance
Immature	F	Ovary small, thin, light pink, slight vascularization. GSI range: 0.39–0.55.	Only primary oocytes present; no atretic oocytes. Lamellar margin thin.
	M	Testes small, thin, light grey, appearance similar to mesentery.	Only primary spermatogonia present.
Regressed	F	Ovary small, light pink, vascularization more obvious than in immature fish. GSI range: 0.39–1.16.	Primary chromatin nucleolar and early perinuceolar stage oocytes. Some atretic oocytes. Lamellar margin thicker than immature, more convoluted.
	M	Testes small, thin, white, slightly larger than immature fish. GSI range: 0.04–0.20.	Primary and secondary spermatogonia present.
Early developing	F	Ovary similar to regressed fish but slightly larger. GSI range: 0.80–1.26.	Appearance of late perinucleolar oocytes and primary cortical alveoli stage oocytes. No atretic oocytes present.
	M	Testes similar to regressed fish but slightly larger. GSI range: 0.16–0.48.	Many secondary spermatogonia and primary spermatocytes.
Developing	F	Ovary visably enlarged, light yellow, highly vascular, approximately 60% of the length of the body cavity. GSI range: 0.95–2.6.	Oocytes in secondary cortical alveolar stage and yolk granule stage. Many oocytes still in primary cortical alveolar stage. Early yolk globular stage present.
	M	Testes thickened, creamy white, no free milt expelled when cut. GSI range: 0.21–0.68.	All stages of spermatogenesis present, with few primary spermatogonia and free spermatozoa. Primary and secondary spermatocytes predominate.
Mature	F	Ovary large, brilliant yellow orange, oocytes visible to naked eye, vascularization prominent. Ovaries 80–90% length of body cavity. GSI range: 2.5–9.6.	Oocytes in yolk globular stage most common. Yolk and oil globules begin to encroach on nucleus. Largest oocytes range from 300 to 375 μm.
	M	Testes creamy white, thicker, more firm and elongated than developing testes. A small amount of milt expelled when cut. GSI range: 0.54–1.42.	No primary spermatogonia present, some secondary spermatogonia. Secondary spermatocytes and spermatids most numerous. Spermatozoa in central lobules.
Ripe	F	Oocytes hydrated, ovary looks clear, takes up almost entire body cavity, highly vascularized. GSI range: 12.5–19.9.	Many hydrated oocytes, irregularly shaped, eosinophilic. Other oocytes in yolk granular and yolk globular stages.
	M	Testes white, swollen, milt does not flow with light pressure, but flows freely when cut. GSI range: 1.07–1.62.	Spermatozoa, spermatids and secondary spermatocytes predominate. Few to no spermatogonia. Central lobules filled with spermatozoa.
Running ripe or spawning	F	Hydrated oocytes expelled with little to no pressure, ovary fluid, fills almost entire body cavity. GSI range: 7.7–17.6.	Same as ripe ovaries but fewer hydrated oocytes. Atretic and postovulatory follicles may be present.
	M	Testes creamy white, milt freely flowing with slight pressure. GSI range: 1.41–3.84.	Same as ripe fish, but spermatozoa evident in sperm ducts.
Partially spent	F	Ovary looks similar to mature condition but more flacid; occupies smaller percentage of body cavity. GSI range: 2.0–5.3.	Similar to mature ovary, except atretic oocytes in several stages of degeneration always evident. Postovulatory follicles occasionally present.
	M	Tests looks the same as running ripe but smaller. GSI range: 0.85–1.77.	No spermatogonia, few primary spermatoocytes. Most active spermatogenesis in peripheral lobules. Spermatozoa partially filling lobules and abundant in sperm ducts.
Spent	F	Ovary flacid but still highly vascularized, no longer than 50% of body cavity, pinkish in color. GSI range: 1.33–2.63.	Massive atresia of all remaining vitellogenic oocytes. Many primary and chromatin nucleolar oocytes present. Lamellar membrane highly convoluted.
	M	Testes flacid, width reduced, white. GSI range: 0.13–0.80.	Spermatozoa present in some lobules. Most lobules small, with only primary and secondary spermatogonia.

glacial acetic acid), and vigorously shaken for 30 seconds. Within a few minutes the cytoplasm cleared and the germinal vesicle could be easily observed microscopically. Ovarian fragments were taken from females collected at the spawning site over a 24-h period, placed in clearing solution and then examined under low-power magnification to determine the stage of final oocyte maturation.

Oocyte Size-Frequency Distributions and Estimates of Batch Fecundity

To determine fecundity and the frequency distribution of oocyte diameters, a 2–15 g piece of tissue was removed from the midsection of the ovaries of 57 fish and weighed to the nearest 0.01 g. The tissues were placed in a modified Gilson's solution (Bagenal 1966) for 3–12 months and periodically shaken to separate the oocytes from connective tissues. Ovaries containing hydrated oocytes were examined after three months since hydrated oocytes of spotted seatrout began to disintegrate when left in Gilson's solution for a longer period of time.

The volumetric method was used to estimate fecundity (Bagenal and Braum 1971). The oocyte samples were suspended in 500–1,500 mL of water and three replicate 0.5 or 1 mL subsamples were taken. All the oocytes >30 μm were counted, and those >80 μm in diameter (the growing oocytes) in each sample were measured to the nearest 15 μm using an ocular micrometer. A total of 556–1,110 growing oocytes were measured in each sample. The number of resting oocytes (oocyte diameter 30–80 μm) was determined by diluting the original oocyte suspension 1:10, and counting three replicate subsamples. Altogether, the frequency distributions of oocytes from 48 fish were analyzed (3 in developing stage; 9 in mature, spawning not imminent stage; 14 in mature, just prior to spawning stage; and 22 in running ripe stage). Fecundity was calculated following Macer's (1974) formula and expressed as relative fecundity of number of eggs per gram ovary-free body weight. Batch fecundity (BF) is defined as all oocytes >350 μm which were undergoing final oocyte maturation that formed a distinct batch, and all hydrated oocytes. This definition of batch fecundity is in agreement with Hunter and Macewicz's (1985) statement that oocytes undergoing final oocyte maturation may be included as hydrated oocytes when hydration occurs very rapidly.

Spawning of Fish in the Laboratory

Four female and two male spotted seatrout were maintained in a 30,000 L recirculating system. The tank, filtration system and feeding regime of the fish has been described previously (Arnold et al. 1976). The salinity ranged from 25 to 30‰. Spawning was induced by increasing the temperature and photoperiod from wintertime settings of 13°C, 9L:15D to 26°C and 15L:9D (Arnold et al. 1976). The filter boxes were checked daily for the presence of buoyant, newly fertilized eggs.

Statistical Analysis

Simple linear regression, oneway analysis of variance, and analysis of covariance were computed for the data using SPSS packaged programs (SPSS 1981).

RESULTS

Size at Maturity

Some female spotted seatrout were sexually mature after they reached 231 mm SL and >90% of the females had reached sexual maturity at 271 mm SL (Table 2). By 300 mm SL, all female spotted seatrout were sexually mature. Fish 300 mm SL or larger made up 85.4%, and immature fish comprised 6.5%, of all the females sampled.

Male spotted seatrout reached sexual maturity at a much smaller size than females. The size at

TABLE 2.—Number and percentage of mature female and male spotted seatrout by 10 mm size categories collected in South Texas, April 1982–May 1985. Maturity was judged by histological and macroscopic inspection.

Standard length (mm)	Female		Male	
	N	% mature	*N*	% mature
201–210	5	0	5	100
211–220	4	0	4	100
221–230	4	0	1	100
231–240	4	50	3	100
241–250	6	83	3	67
251–260	6	100	5	100
261–270	5	80	7	100
271–280	11	91	10	100
281–290	14	100	11	100
291–300	24	96	20	100
301–310	60	100	40	100
311–320	94	100	68	100
321–330	115	100	80	100
>330	945	100	507	100
Total	1,297		764	

which most male spotted seatrout attain sexual maturity could not be determined, since the smallest fish collected by the sampling methods (200 mm SL) were all sexually mature (Table 2).

Season and Time of Spawning

Histological and macroscopic examination of the gonads (see Table 3 and Figure 3) and mean GSI values (Fig. 2) show that spotted seatrout have an extended reproductive season in South Texas. Mean GSI values of males and females increased by April 1982–85 and remained elevated through the end of September. A 5°C increase in water temperature at the sampling sites to 23°C during the first week of April 1982–85 was paralleled by an increase in GSI to 2.1 in males and 4.5 or greater in females. The pattern of seasonal changes in mean GSI values of males was relatively consistent during the three-and-a-half years of sampling. Mean GSI values began to increase in mid-February, reached a maximum of 1.9–2.4 by April, and slowly declined during the spawning season until they dropped rapidly to regressed levels of 0.2 by the first half of October (Fig. 2). The seasonal patterns in mean GSI values of females were also similar from 1982 to 1985. In all four years, mean GSI increased in April and subsequently declined in May. In 1982–84, mean GSI increased again later in the season prior to the final decrease to regressed levels in October (Fig. 2). Thus, mean GSI values appear to be bimodal, with one period of peak spawning activity in April, and the second period of peak spawning activity varying between August 1982 and July 1983 and 1984.

Male and female spotted seatrout in spawning condition (males with freely flowing milt, females with ovulated oocytes) were consistently captured during a 2-h period around dusk over shallow (1 m) beds of *Thalassia testudinum* or *Halodule wrightii* bordered by a channel 2 m deep. The salinity at the spawning sites ranged from 20 to 37‰. Although actual spawning was not observed, collection of newly fertilized eggs from the spawning area at dusk confirmed that spawning was taking place (Holt and Holt[4]). Spawning fish were not captured over beds of scattered *H. wrightii* or *T. testudinum* that were not immediately adjacent to a channel. Females with freely

[4]S. A. Holt and G. J. Holt, University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, pers. commun. 1983.

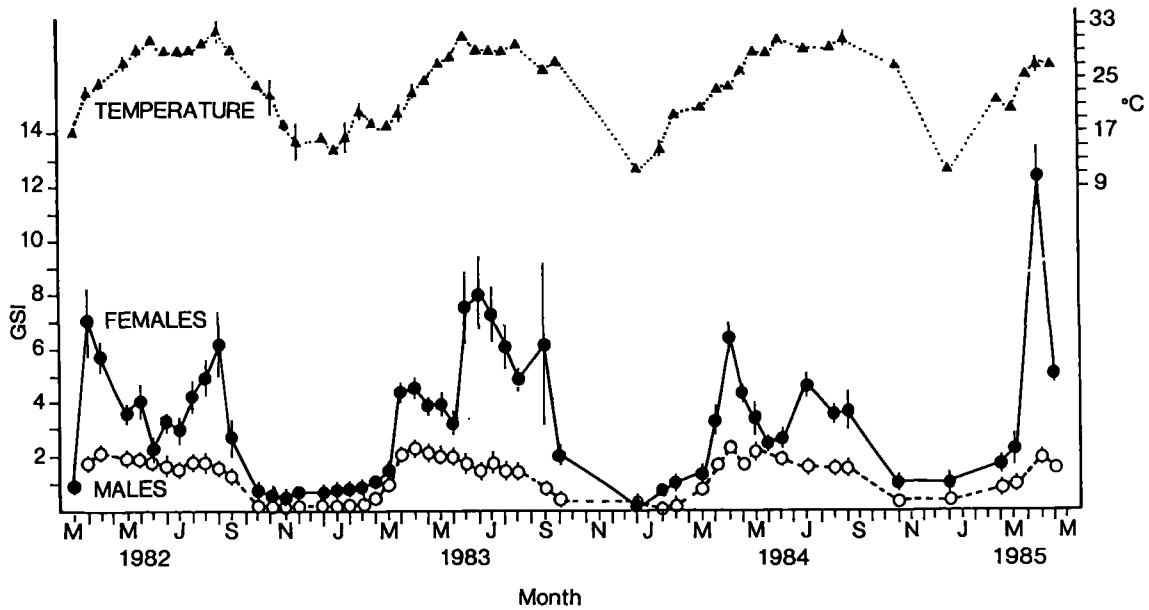

FIGURE 2.—Bi-monthly mean water temperature and mean gonadosomatic index (GSI) of male and female spotted seatrout collected in South Texas from March 1982 to May 1985, including ±1 SE of the mean. Sample size for each data point: 3–61 for females (sample size <15 in only 9 cases) and 2–52 for males (sample size <9 in only 9 cases).

flowing oocytes were only captured at dusk and milt appeared to flow more freely in males at dusk than at other times of the day.

Gonadal Development in Males

Testicular recrudescence began in January with the appearance of primary spermatocytes (Fig. 3), and by February the majority of the males were in the early developing or developing reproductive stage. In March, 89% of the males had testes containing free spermatozoa (Fig. 3), although only 27% were running ripe. Over 94% of all males captured from April until the end of August were running ripe. Spent males first appeared in August and all the males during October and November were either in the spent or regressed condition. In December, all males captured had regressed testes containing only primary and secondary spermatogonia (Fig. 3).

Histological observations revealed that the testes are the common unrestricted spermatogonia type, as described by Grier (1981). Spermatogenesis occurred throughout the entire testis during the majority of the year. However, from late February through early August, spermatogenesis was more advanced in the central lobules then in the peripheral lobules. By August there was no spermatogenic activity in the central lobules, although spermatogenesis continued in the peripheral lobules until mid-September. The only period of the year when there was no active spermatogenesis was from October through late January, although primary and secondary spermatogonia were present from October through the end of April (Fig. 3). Primary spermatocytes were common from late January until March, although they did not disappear from the testes entirely until the end of July. Secondary spermatocytes first appeared in mid-February, were common through the end of July and did not disappear until early September (Fig. 3). Spermatids and spermatozoa were present in the central lobules by late February, and from March through mid-August the central lobules were swollen with spermatozoa (Fig. 3). In late August and September many of the central lobules appeared to be partially empty of spermatozoa, although some spermatozoa were still present up to mid-November (Fig. 3). The peripheral lobules contained active spermatogenic cysts of primary and secondary spermatocytes during June and July and the lumens of these lobules began to fill with spermatozoa. The peripheral lobules were swollen with spermatozoa during August and September, but by mid-October no spermatozoa remained.

Gonadal Development in Females

Gonadal recrudescence was observed in a small percentage of the females captured in January and by March 94% of the females were undergoing ovarian development (Table 3). Fish with mature ovaries were found from March until the end of September, while running ripe fish were captured from April through the end of September (Table 3). Partially spent fish (females that appeared to have spawned at least once but still contained vitellogenic oocytes) were captured from May through the end of September. No com-

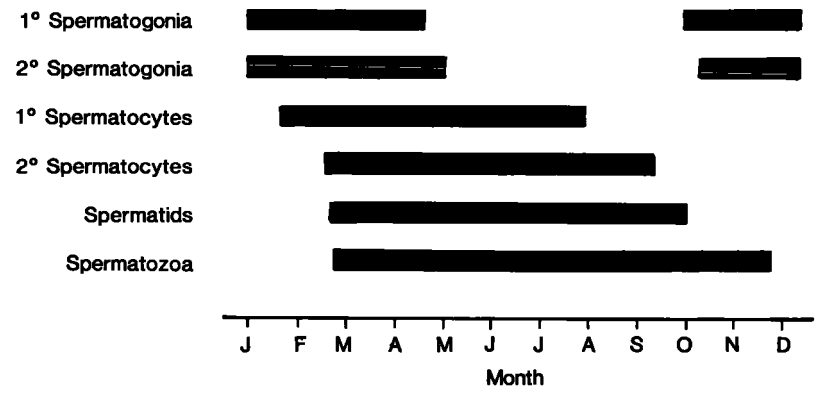

FIGURE 3.—Seasonal cycle of spermatogenesis in spotted seatrout collected in South Texas, as determined by histological and macroscopic observations. Data from April 1982 through mid-May 1985 are combined. 1° - primary, 2° - secondary.

TABLE 3.—Percentage of female spotted seatrout in seven reproductive stages by month, as assessed by histological and macroscopic examination of the ovaries. Data from April 1982 to May 1985 are combined. REG = Regressed, E DEV = Early Developing, DEV = Developing, MAT = Mature, RR = Ripe and Running Ripe, P SP = Partially Spent, SP = Spent.

		Percent in each reproductive stage						
Month	*N*	REG	E DEV	DEV	MAT	RR	P SP	SP
January	70	98	2					
February	51	55	43	2				
March	124	4	56	31	9			
April	372		4	6	78	12		
May	220			4	84	5	7	
June	104			1	56	19	24	
July	114		1		48	30	20	1
August	100				58	32	7	3
September	37	14			37	30	11	8
October	8	87						13
November	27	100						
December	51	98			2			
Total	1,278							

pletely spent fish were captured before July and few were captured during the remainder of the reproductive season.

Histological observations of fish with regressed ovaries collected from late September to mid-February showed only primary chromatin nucleolar and early perinucleolar oocytes. Atretic oocytes were present from September until mid-December; no atretic oocytes were observed from mid-December through the end of February. The appearance of late perinucleolar and primary cortical alveoli stage oocytes in late January, February, and early March represented the initial stages of ovarian recrudescence. Ovarian development was proceeding rapidly by early March and oocytes in the secondary cortical alveoli and yolk granule stages were common.

During the reproductive season, histological observations of the ovary showed a heterogeneous morphology. Oocytes in all stages of growth (from resting to the fully grown yolk globular stage) were distributed throughout the ovaries of all mature, running ripe, and partially spent fish collected from March through the end of September. Vitellogenesis was probably continuous from February until the end of September, as shown by the continual presence of large numbers of oocytes in the cortical alveoli and yolk granule stages. The relative percentages of three types of post cortical alveolar stage oocytes in fish in the mature reproductive stage did not change markedly from March through the end of September (Fig. 4). The percentage of oocytes in the yolk granule stage (diameter in histological preparations: 150–190 μm) varied from a low of 7.3% in June to a late season high of 16.1%, and averaged 13% of the total number of oocytes in the ovary. Yolk globular oocytes, the largest oocytes present (diameter: 200–375 μm), were most common. The percentage of oocytes in the yolk globular stage ranged from a high of 30.8% in April to an end-of-season low of 22.6% in September and averaged 26.9% during the reproductive season. In addition to the actively growing oocytes in the ovary, a small percentage of atretic oocytes was always found in fish with mature ovaries. Atretic oocytes are defined here as vitellogenic oocytes undergoing alpha stage atresia. The percentage of atretic oocytes ranged from a low of 2.2% in March to a midsummer high of 8% in July and averaged 5.4%. Additionally, postovulatory follicles (POF) were observed in the ovaries of fish captured from

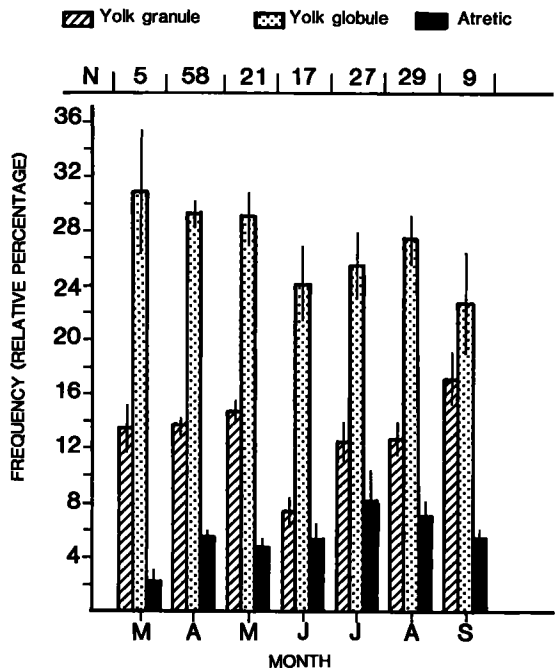

FIGURE 4.—Frequency of three different types of oocytes in female spotted seatrout ovaries in the mature reproductive stage (MAT, Table 3) as assessed by histological observation. Fish were collected from South Texas during the reproductive season. Frequency refers to the percentage of each type of oocyte relative to the total number of all types of oocytes counted. Data from April 1982 through the end of September 1983 are combined and the number (*N*) of individuals examined each month is indicated. Bars indicate mean percentage of oocytes ±1 SE of the mean. Yolk granule oocyte diameters ranged from 150 to 190 μm, and yolk globule oocyte diameters ranged from 200 to 375 μm in histological preparations. Atretic oocytes are defined here as oocytes in alpha stage atresia.

April through September, although the percentage of POF relative to the total number of oocytes was always small (<5%).

The histological appearance of the zona radiata and follicle layers changed as the oocytes developed. The zona radiata (chorion) was thin and nonstriated in perinucleolar and cortical alveoli oocytes. The zona radiata started to take on its characteristic striated appearance when oocytes reached the yolk granular stage and became noticeably thicker and more striated as oocytes grew into the yolk globular stage. In contrast, the granulosa and thecal layers appeared to decrease in thickness as oocyte development proceeded. Oocytes in the perinucleolar and cortical alveoli stages had thick, well-developed granulosa and thecal layers. In yolk granular and yolk globular oocytes, both follicle layers were noticeably thinner and the thecal layer was not always continuous around the oocyte.

Frequency distributions of growing oocytes (diameters in Gilson's solution >80 μm; perinucleolar to hydrated stage oocytes) from ovaries of 48 fish were analyzed, and Figure 5 shows typical patterns in fish from four reproductive stages. In a fish captured in March with developing ovaries, growing and vitellogenic oocytes (oocytes during the phase of active vitellogenin uptake) ranging from 80 to 185 μm in diameter were present (Fig. 5A; 625 oocytes counted). Fish in the mature reproductive stage in which spawning did not appear to be imminent, as indicated by GSI values <4, had growing and vitellogenic oocyte diameters ranging from 100 to 320 μm (Fig. 5B; 556 oocytes counted), comprising 21% of the total number of oocytes >30 μm in the ovary. Fish just prior to spawning, as indicated by GSI values >7, had a distinct batch of oocytes with diameters >350 μm that were undergoing final oocyte maturation (Fig. 5C; 585 oocytes counted). However, there were no other distinct modes of vitellogenic oocytes. In running ripe fish, the batch of large oocytes hydrated to a diameter of 520 μm or greater (Fig. 5D; 1,110 oocytes counted). The results (Figs. 5A–D) clearly demonstrate that *C. nebulosus* has a continuous distribution of growing and vitellogenic oocytes. The oocyte frequency distribution of the vitellogenic oocytes <320 μm in diameter remaining in running ripe fish ap-

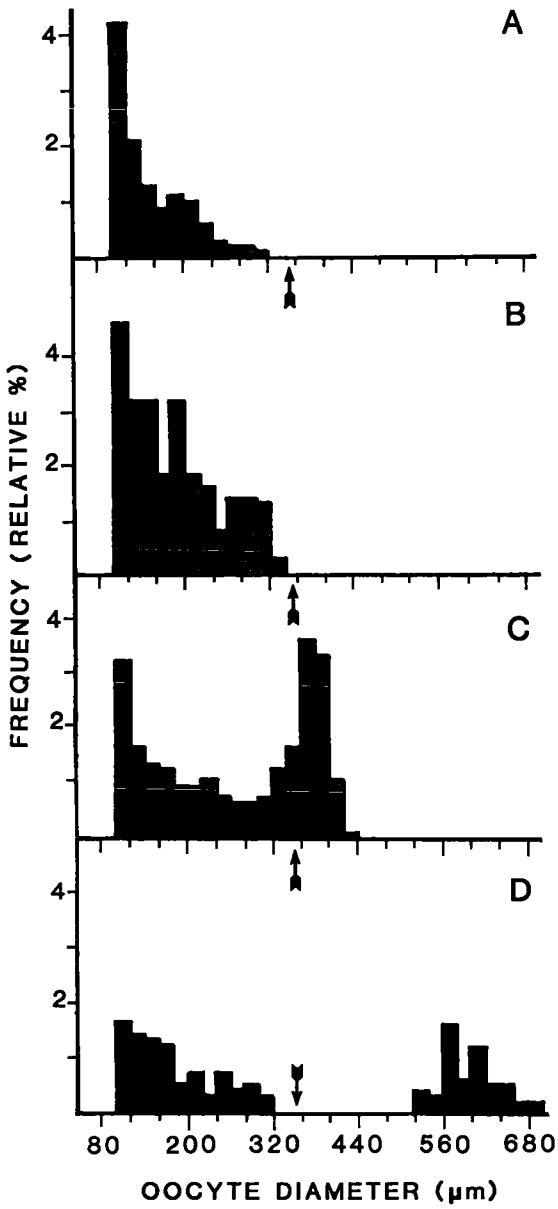

FIGURE 5.—Frequency distributions of growing oocyte diameters (>80 μm) in female spotted seatrout collected from South Texas. Growing oocytes comprised 21% of the total number of oocytes >30 μm in the ovary. Oocyte diameter refers to the diameters of oocytes after preservation in Gilson's solution. Frequency refers to the percentage of each size of oocyte relative to the total number of oocytes in the subsample. Each graph represents data from a single fish at a different reproductive stage. The arrow at 350 μm indicates the minimum size necessary for final maturation to occur. A. Developing stage in March, GSI = 1.6. B. Mature stage in which spawning is not imminent, GSI = 3.7. Fish in this stage were collected from April through the end of September. C. Mature stage just prior to spawning, GSI = 7.4. Fish in this stage were collected from April through the end of September. D. Running ripe stage, GSI = 17.6. Fish in this stage were collected from April through the end of September.

peared similar to the oocyte distribution in nonspawning fish (Fig. 5B, D). The percentage (21%) of growing and vitellogenic oocytes in the ovary remained constant throughout the reproductive season in fish in the mature and running ripe stages.

Final Oocyte Maturation

Final oocyte maturation (FOM) was highly synchronized in spotted seatrout and occurred only in oocytes >400 μm [5]. Figure 6A shows a photomicrograph of a histological section of a spotted seatrout ovary in the mature reproductive stage that was not undergoing final oocyte maturation. Many oocytes were in the yolk globular stage and appeared to be fully grown. The first readily observable stage of FOM in "cleared" oocytes was lipid coalescence (Fig. 6B). The oil droplets in the oocytes began to coalesce around the germinal vesicle (nucleus) and subsequently formed one to three large oil droplets. This stage was not always observed in histological preparations since many of the oocytes were not sectioned through their centers. The yolk globules remained discrete during lipid coalescence. After the lipids had coalesced, the germinal vesicle (GV) began to migrate to the periphery of the oocyte (germinal vesicle migration, or GVM). GVM could be seen in both histological sections (Fig. 6C) and in "cleared" oocytes (Fig. 6D). The oil droplet occupies the center of the oocytes shown in Figure 6C, D. Histological observation of this stage (Fig. 6C) showed that the yolk globules were not coalesced, the oil droplets had coalesced to form one or two large droplets and the GV had begun to lose its integrity and often appeared semicircular. At the completion of GVM, the nuclear (germinal vesicle) membrane broke down (GVBD) and the nuclear material intermingled with the cytoplasm of the oocyte. Hydration occurred shortly thereafter, followed by ovulation and spawning of the fully mature oocyte.

Final oocyte maturation occurred within 10 hours in spotted seatrout in the natural environment (Fig. 7). A total of 209 fish were collected over eight 24-h periods from April through August in 1984 and 1985. Forty-three percent of the fish collected between the hours of 0500 and 1500 were undergoing FOM. Lipid coalescence was first observed at dawn (0545), and GVM started at 0900. By 1430, all fish undergoing final maturation had hydrated oocytes and ovulation and spawning commenced at dusk (1830) and continued until 2100. None of the fish collected from 2100 to 0500 were undergoing FOM.

Batch Fecundity

The significant positive relationship ($P < 0.001$) between BF and ovary-free body weight can be best described by the following equation: $BF = 459WT - 56{,}066$, $r^2 = 0.56$ (Fig. 8), while curvilinear equations best described the relationship between BF and SL and TL. The coefficients of determination in all cases were <0.56.

A one-way analysis of variance showed that mean BF (number of eggs per gram ovary-free weight) did not vary significantly during the April through September spawning season. Mean relative batch fecundity was highest in September, lowest in May, and varied little during April, June, and July (Table 4).

A prominent batch of oocytes was present only in females that were in all stages of final oocyte maturation or were running ripe (Figs. 5C, D; 7). The average batch size calculated from 14 fish containing hydrated oocytes and no postovulatory follicles was 451 ± 43 eggs/g ovary-free body weight. This number averaged 15.5 ± 2.5% of the number of growing and vitellogenic oocytes in the ovary.

TABLE 4.—Monthly mean batch fecundity expressed as number eggs/g ovary-free body weight of spotted seatrout in South Texas. All means were not statistically different.

Month	N	Mean fecundity ±1 SE
April	19	477 ± 42
May	2	320 ± 72
June	3	435 ± 109
July	5	409 ± 76
August	3	361 ± 60
September	3	560 ± 79

Spawning Frequency

To estimate the spawning frequency of spotted seatrout in South Texas, the percentage of running ripe females captured monthly from April through the end of September in 1982 through 1985 was examined. Only fish captured at dusk and >305 mm SL were included in this analysis. The percentage of spawning females ranged from

[5] A 400 μm live oocyte equals a 350 μm oocyte preserved in Gilson's solution. Both measurements represent oocytes beginning FOM.

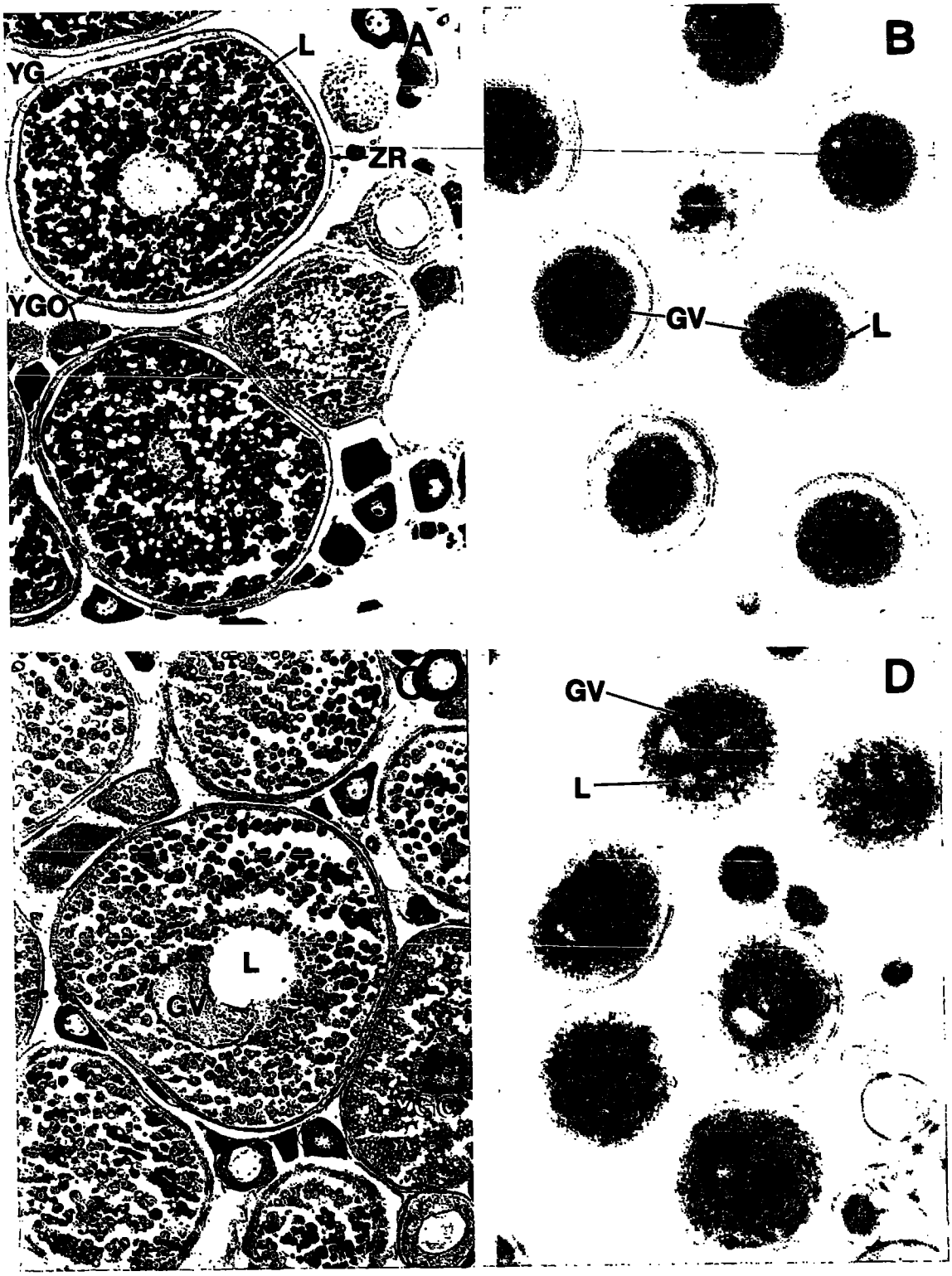
A
L
YG
ZR
YGO
B
GV
L
L
GV
D
GV
L

FIGURE 6.—Photomicrographs of oocytes from spotted seatrout in the mature reproductive stage collected from South Texas. A. Histological section of an ovary in the mature stage that is not undergoing final oocyte maturation (FOM). Oocyte development is continuous, with fully grown yolk globular oocytes co-occurring with oocytes in earlier stages of development (Magnification 120×). B. "Cleared" oocytes in the lipid coalescence stage, the first stage of FOM (magnification 40×). C. Histological section of an oocyte undergoing germinal vesicle migration (GVM). (Magnification 160×). D. "Cleared" oocytes in the GVM stage (magnification 40×). Key: GV = germinal vesicle or nucleus, L = Lipid droplets, YG = yolk globules, YGO = yolk globular oocyte, ZR = Zona radiata.

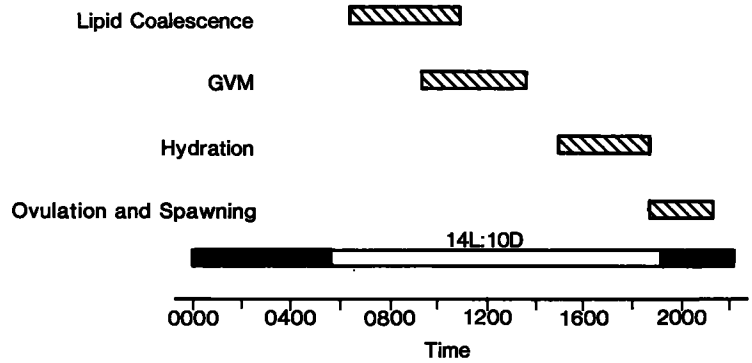

FIGURE 7.—Time-course of final oocyte maturation in spotted seatrout collected from South Texas. Lipid coalescence is the initial stage in final oocyte maturation. Data obtained from 46 fish undergoing final oocyte maturation in April and May 1985. GVM = germinal vesicle migration. 14L: 10D = hours of light and dark.

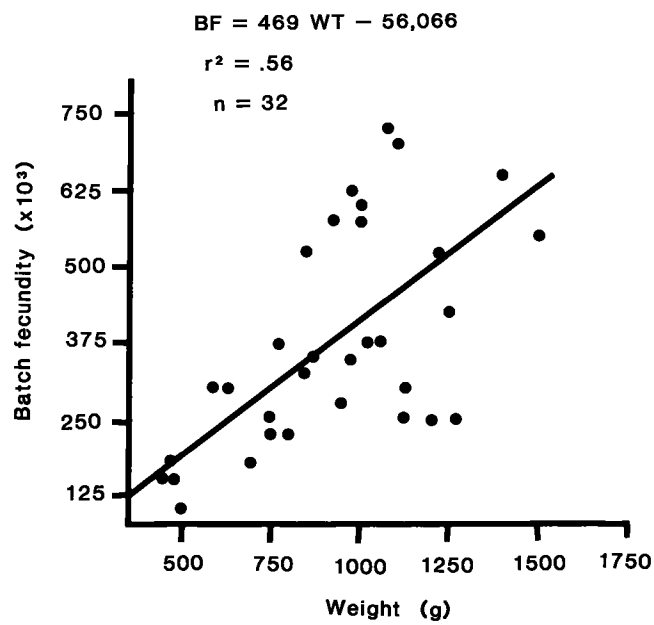

FIGURE 8.—Relation between batch fecundity (BF) and ovary-free body weight (WT) of spotted seatrout from April 1984 to May 1985. Thirty-three fish with oocytes >350 μm that were undergoing final oocyte maturation and formed a distinct batch of oocytes or had hydrated oocytes are included.

a low of 8% in May to a high of 45% in September (Table 5). An average of 27.5% of the females captured during the spawning season were running ripe, corresponding to an average spawning frequency of once every 3.6 days or 50 times during the 6-mo spawning period.

The spawning frequency was also estimated from females that were undergoing final oocyte maturation (FOM) between the hours of 0600 and 1400 in April, May, July, and August 1984 and 1985 (Table 5). For comparison, the actual percentage of running ripe females captured during the same months is also presented. An average of 42.8% of the females examined for final oocyte maturation from April through August were undergoing FOM. Therefore, average spawning frequency was once every 2.3 days, or 80 times during the 6-mo spawning season.

Spawning frequency was also estimated from the percentage of females captured with ovaries containing postovulatory follicles (POF). An average of 13.1% of the females captured had ovaries which contained POF ranging from 12 hours to 2 days old. This would correspond to a spawning frequency of once every 7.6 days or 24 times during the spawning season.

Finally, the spawning frequency of four female *C. nebulosus* in the laboratory under conditions of controlled temperature and photoperiod were examined (Table 6). The fish spawned from 1 to 10 times each month for 17 months, an average of 17 spawns per individual over a 12-mo period (Table 6). This would correspond to a spawning frequency of once every 21 days.

TABLE 5.—Percentage of spotted seatrout spawning (RR) or undergoing final oocyte maturation (FOM) in South Texas. Data on spawning fish collected April 1982–May 1985. Data on fish undergoing FOM collected April 1984–May 1985.

	Spawning fish 1982–85			Fish undergoing FOM 1984–85			
Month	*N*	# RR	% RR	*N*	# FOM	% FOM	% RR
April	256	42	16	33	14	42	37
May	140	11	8	21	10	48	13
June	101	20	20	—	—	—	—
July	82	33	40	7	3	43	52
August	101	36	36	8	3	38	—
September	20	9	45	—	—	—	—
Mean			27.5			42.8	25.5

TABLE 6.—Number of spawns and average water temperature by month for four female spotted seatrout contained in a 30,000 L tank in Port Aransas, TX, under conditions of controlled temperature and photoperiod, July 1974–November 1975. Experimental procedures described in Arnold et al. (1976).

Month	Number of spawns	°C
July	8	26.75
August	7	26.75
September	4	26.0
October	6	25.5
November	4	24.5
December	8	24.0
January	9	23.5
February	10	24.0
March	10	24.0
April	3	25.75
May	1	25.0
June	0	22.0
July	6	25.75
August	2	25.0
September	2	23.0
October	9	23.5
November	10	24.0
Total	99	
Average: 17 spawns/ 12 months/ female		

DISCUSSION

Sexual Maturity and Spawning Season

Male spotted seatrout reached sexual maturity at a smaller size than females which appears to be a fairly common phenomenon in spotted seatrout throughout its range (see Mercer 1984 for a review). Both male and female spotted seatrout in South Texas reached sexual maturity at a size similar to that reported for other groups of *C. nebulosus* along the Gulf Coast (Moody 1950; Klima and Tabb 1959; Overstreet 1983) and at a smaller size than along the East Coast (Tabb 1961; Brown 1981).

Running ripe females were captured only between one hour before and two hours after sunset in South Texas, suggesting a high degree of synchrony in spawning fish. Collections of newly fertilized eggs during a $2\frac{1}{2}$-h period after sunset (Holt et al. 1985) provides supporting evidence for this spawning synchrony.

Both histological data and GSI values showed spotted seatrout have an extended spawning season in South Texas. Gonadal recrudescence began in January in male and in February in female spotted seatrout. Spawning commenced in April and continued until the end of September. Other studies of *C. nebulosus* along the Gulf and East coasts of the United States have also reported long spawning seasons (Mercer 1984). Additionally, other sciaenids have extended spawning seasons (Merriner 1976; White and Chittenden 1977; DeVries and Chittenden 1982; Love et al. 1984),

suggesting a prolonged spawning season is a common reproductive strategy among sciaenids living in temperate and subtropical waters.

The duration of the spawning season may be related to water temperature. Perhaps this apparent association with temperature is related to the viability and development of spawned spotted seatrout eggs. Twenty-three degrees may be the minimum temperature necessary for successful spawning, as indicated by both the failure to capture running ripe fish at lower temperatures and by data from spotted seatrout induced to spawn under laboratory conditions (Arnold et al. 1976; Table 6). However, since spawning ceased in September when water temperatures were well above 23°C, possibly a decrease in photoperiod in combination with a decrease in temperature provides the necessary cue for termination of spawning. Hein and Shepard (1979) suggested photoperiod may be an important regulating factor in *C. nebulosus* spawning. Data from laboratory-spawned spotted seatrout (Arnold et al. 1976) also support this speculation.

The seasonal pattern of mean GSI values during the spawning season was relatively consistent for both males and females over the $3\frac{1}{2}$-yr period, 1982–85 (Fig. 2). The bimodality of the female GSI data suggests the possibility of two peaks in spawning activity, although the timing of the second peak varies from year to year, thus demonstrating the need for several consecutive years of data. Bimodal spawning peaks have been previously reported for the species by Hein and Shepard (1979) in Louisiana, Stewart (1961) in Florida, and Brown (1981) in Chesapeake Bay, VA. However, mean GSI values should be used with caution when attempting to predict actual peaks in spawning activity (deVlaming et al. 1982).

Fecundity

Accurate annual fecundity measurements are difficult to determine for multiple spawning fishes with an extended spawning season. Methods of calculating annual fecundity from measurements of the total number of growing oocytes at the beginning of the spawning season (Bagenal 1966), or other approaches based on the total number of oocytes at the beginning of the spawning season minus egg retention at the end of the spawning season (Conover 1985), are inappropriate for multiple spawning species such as spotted seatrout which show continuous recruitment of oocytes during the reproductive season. Thus, the previous estimates of annual fecundity in spotted seatrout, which did not take continuous recruitment of oocytes into consideration and measured either total fecundity (Overstreet 1983) or fecundity of growing and vitellogenic oocytes (Sundararaj and Suttkus 1962), probably underestimated annual fecundity. Furthermore, BF has not previously been calculated for this species.

Although no monthly differences in BF were apparent (Table 4), sample sizes were too small to draw any definite conclusions from these data. The relatively low coefficient of determination (0.56) is similar to values reported by Conover (1985) for Atlantic silversides, *Menidia menidia*, another multiple spawning species. Perhaps a more accurate estimate of annual fecundity than previously reported for spotted seatrout can be obtained by multiplying BF by the number of spawns during the reproductive season. Unfortunately, as discussed later, estimates of spawning frequency vary considerably, so it is not possible to make an accurate estimation of the annual fecundity. However, available data indicate that average annual fecundity may be greater than 10 million eggs.

Multiple Spawning

Histological examination of the testes revealed that spermatogenesis ceased earlier in the central lobules, although they contained spermatozoa one-and-one-half months longer than the peripheral lobules. It is possible that the same central lobules act as storage areas for spermatozoa produced by the more spermatogenically active peripheral lobules during the second half of the spawning season, as suggested by Hyder (1969) for *Tilapia*. This may represent a strategy in multiple spawning fish with a prolonged spawning season that allows for a constant supply of spermatozoa while investing a minimal amount of energy into spermatogenesis.

Several lines of evidence indicate that female *C. nebulosus* also spawn several times during the reproductive season. The relatively high percentage of running ripe females, fish undergoing FOM and partially spent fish captured throughout the spawning season, and the absence of completely spent fish until the last third of the spawning season, suggest that an individual does not spawn all the vitellogenic eggs in the ovary at one time. Indeed, oocyte size-frequency analysis shows a continuous distribution of growing and

vitellogenic oocytes (Fig. 5) and fecundity estimates show that only about 15% of the growing oocytes undergo FOM prior to a spawn. Histological data shows that the percentage of vitellogenic oocytes in the ovary remains constant throughout the spawning season (Fig. 4), which suggests that new oocytes may be recruited into the vitellogenic phase as rapidly as mature oocytes are released. Convincing histological evidence of multiple spawning is the presence of postovulatory follicles (POF) from May through the end of September in ovaries containing many vitellogenic oocytes. Hunter and Goldberg (1980) characterized postovulatory follicles in laboratory-spawned *Engraulis mordax*, a multiple spawning fish, and found POF in all females that had spawned in the laboratory one or two days previously. Finally, laboratory studies also show that spotted seatrout are capable of multiple spawning under relatively constant environmental conditions (Table 6). Tucker and Faulkner (1987) also found that six female fish kept in raceways outdoors at the ambient summer temperature and photoperiod spawned repeatedly.

Spawning Frequency

It is especially difficult to determine the spawning frequency of wide-ranging, multiple-spawning marine fishes such as *C. nebulosus* that are not group-synchronous spawners. One method to estimate spawning frequency is to count the number of distinct batches of vitellogenic oocytes in the ovary (Shackley and King 1977). However, only one distinct batch of vitellogenic or hydrated oocytes can be distinguished in spotted seatrout ovaries at any one time (Fig. 5) and the reliability of this method has been questioned (deVlaming 1983). Therefore, three techniques were used to estimate spawning frequency in spotted seatrout.

Spawning frequency was estimated to be once every 3.6 days from the percentage of running ripe fish caught on the spawning grounds. Although this is probably an overestimate owing to sampling bias, the error may not be susbtantial, since the spawning grounds are also the feeding grounds for this species (Moody 1950) and many nonspawning individuals were captured. The time of sample collection did not significantly influence the estimate of spawning frequency. High spawning frequencies were also obtained (every 2.3 days) when fish were captured 6–12 hours prior to spawning and examined for signs of final oocyte maturation (Table 5). The spawning frequency of other sciaenids fishes has been estimated by this technique (DeMartini and Fountain 1981; Love et al. 1984). Additionally, Hunter and Macewicz (1985) suggested that this method produces a useful first approximation of spawning frequency.

The proportion of fish having POF in the ovary has also been used to determine spawning frequency (Hunter and Goldberg 1980; Alheit et al. 1984; Hunter and Macewicz 1985). Spotted seatrout were found to have POF throughout the spawning season, although the age of the POF was often difficult to determine. Furthermore, detailed laboratory studies have not been undertaken to accurately age POF in spotted seatrout. However, the once a week estimate of spawning frequency obtained using this method is similar to spawning frequencies reported for two other sciaenids, the queenfish, *Seriphus politus*, (DeMartini and Fountain 1981) and the white croaker, *Genyonemus lineatus*, (Love et al. 1984). Spawing frequency estimates from POF are probably more reliable than estimates based on the number of spawning fish since sampling bias is less likely to occur when capturing fish with POF.

Another method used to quantify spawning frequencies in various species is direct observation of spawning in the laboratory or in "controlled" field situations, such as impoundments (Gale and Deutsch 1985; Hubbs 1985; Heins and Rabito 1986). Spotted seatrout spawned an average of once every three weeks per individual under controlled temperature and photoperiod in the laboratory (Table 6). Tucker and Faulkner (1987) found that six female spotted seatrout kept outdoors at ambient temperature and photoperiod averaged one spawn per individual every 2.3 weeks. The same spawning frequency was noted for an individual female, although that same individual later spawned three times in four days (Tucker and Faulkner 1987). Thus, spotted seatrout appear to be capable of the high spawning frequencies estimated from field-caught fish with hydrated ovaries, although this frequency is probably not sustained throughout the entire spawning season. In general, the spawning frequencies in both laboratory studies are lower than those estimated from actual spawning fish in the field. However, it is unclear whether this is due to an overestimation of spawning frequency in the field or to a decline in spawning frequency owing to confinement in the laboratory.

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TABLE 1.—Results of nearshore cruises using two types of shrimp trawls.

Cruise dates	Net type	Sampling[1] strategy	Sample area[2]	Total net-hour	No. Spanish	No. kings
July–Sept. 1980	semiballoon	SR+NR	NC, SC, GA, FL	114	250	40
Apr.–June 1981	semiballoon	SR	NC, SC, GA, FL	77	21	13
Sept. 1982–Jan. 1983	semiballoon	SR	NC, SC, GA, FL	73	27	27
Aug.–Sept. 1985	semiballoon	SR+NR	NC, SC, GA, FL	59	120	36
Aug.–Sept. 1986	tongue	NR	NC, SC, GA, FL	41	1,421	104
Oct. 1986	tongue	SR	NC, SC, GA	55	681	481
July–Aug. 1986	tongue	NR	SC	20	2,303	84
Sept.–Oct. 1986	tongue	NR	SC	20	327	80

[1]SR = stratified random sampling; NR = nonrandom sampling.
[2]At least some portions of the waters of these states were sampled.

mackerels taken in tongue nets on two cruises are presented in Figures 1 and 2, respectively. Comparisons of the catch rates of Spanish mackerel during the TED evaluations in July–August 1986 showed that significantly fewer were taken in the tongue net equipped with a NMFS TED than the control net (Mann-Whitney: $P < 0.001$) or the Georgia TED-net ($P < 0.05$) (Table 2). There were no significant differences in catches of king mackerel (Table 3), or in catches of either species between nets on the September–October cruise, perhaps due to the smaller sample sizes.

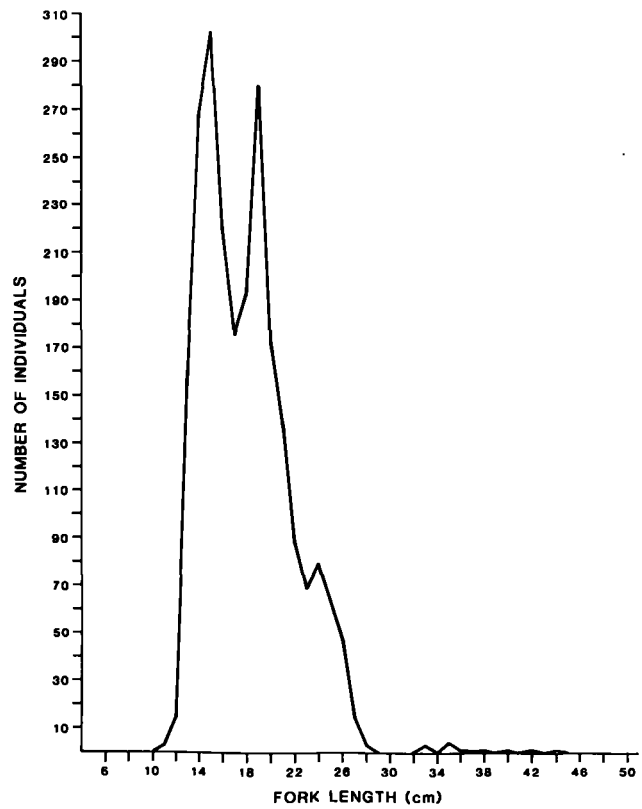

FIGURE 1.—Length-frequency distribution of Spanish mackerel taken in shrimp tongue trawl nets during July–August 1986 along the southern Atlantic coast of the United States (n = 2,303).

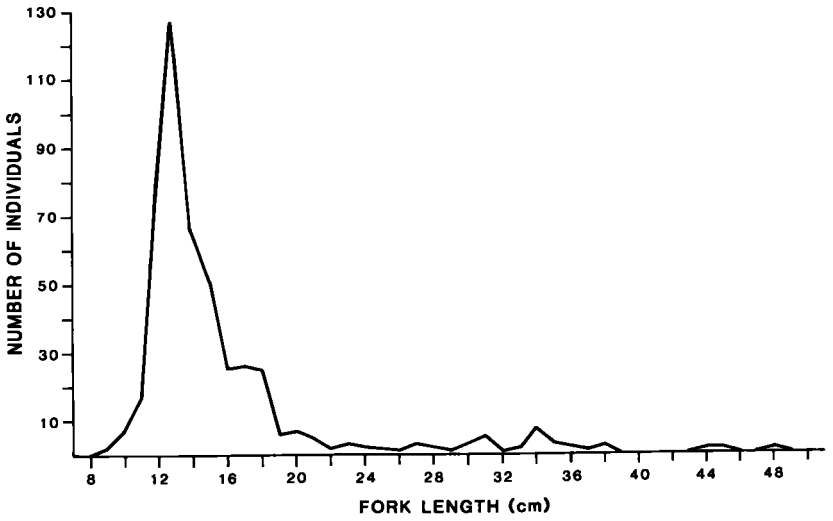

FIGURE 2.—Length-frequency distribution of king mackerel taken in shrimp tongue trawl nets during October 1986 along the southern Atlantic coast of the United States (n = 481).

TABLE 2.—Catches of Spanish mackerel during evaluations of tongue nets equipped with trawl efficiency devices (TED's). C = 22.9 m footrope length tongue net; NMFS = 22.9 m footrope length tongue net with a NMFS TED; GA = 22.9 m footrope length tongue net with a Georgia TED. Tow times = 1 hour.

Cruise	Comparison	No. of tows	Net type	No. of Spanish mackerel			Net type	No. of Spanish mackerel		
				Total	$\bar{x} \pm SD$	Range		Total	$\bar{x} \pm SD$	Range
July–Aug.	C-NMFS	10	C	1,104	110 ± 27	68–144	NMFS	519	52 ± 23	12–73
	C-GA	10	C	1,199	120 ± 65	40–276	GA	1,219	122 ± 74	44–300
	NMFS-GA	10	NMFS	880	88 ± 53	35–176	GA	1,650	165 ± 142	67–533
Sept.–Oct.	C-NMFS	5	C	104	21 ± 15	2–41	NMFS	53	11 ± 11	2–27
	C-GA	5	C	206	41 ± 38	1–103	GA	155	31 ± 28	0–76
	NMFS-GA	5	NMFS	108	22 ± 23	4–58	GA	149	30 ± 25	3–59

TABLE 3.—Catches of king mackerel during evaluations of tongue nets equipped with trawl efficiency devices (TED's). C = 22.9 m footrope length tongue net; NMFS = 22.9 m footrope length tongue net with a NMFS TED; GA = 22.9 m footrope length tongue net with a Georgia TED. Tow times = 1 hour.

Cruise	Comparison	No. of tows	Net type	No. of king mackerel			Net type	No. of king mackerel		
				Total	$\bar{x} \pm SD$	Range		Total	$\bar{x} \pm SD$	Range
July–Aug.	C-NMFS	10	C	41	4 ± 4	1–13	NMFS	46	5 ± 9	0–30
	C-GA	10	C	43	4 ± 5	0–15	GA	41	4 ± 4	0–13
	NMFS-GA	10	NMFS	23	2 ± 3	0–8	GA	26	3 ± 5	0–17
Sept.–Oct.	C-NMFS	5	C	26	5 ± 7	0–15	NMFS	14	3 ± 3	0–5
	C-GA	5	C	40	8 ± 8	4–22	GA	22	4 ± 5	1–14
	NMFS-GA	5	NMFS	24	5 ± 2	2–8	GA	20	4 ± 4	2–11

Discussion

Although it is possible that juvenile mackerels were more abundant in 1986 than in previous years, the increased catches of these fishes in tongue nets over semiballoon nets suggests that the former are much more efficient in capturing these fishes. Preliminary data from a gear comparison cruise in 1987 indicate that tongue nets do catch more pelagic fishes than semiballoon nets even after adjusting for differences in footrope lengths (G. Sedberry[4]). Unfortunately,

[4]G. Sedberry, Marine Resources Research Institute, South Carolina Wildlife and Marine Resources Department, P.O. Box

these tests were conducted during March–April when juvenile mackerels are rare in the coastal waters of South Carolina.

In 1986 we collected juvenile mackerels during July through October. Because of incomplete temporal sampling, we do not know if they were present earlier and later in the year in this region. Based on the occurrence of early larval stages, spawning of both mackerels in the South Atlantic Bight extends from May through at least September (Collins and Stender 1987). If growth rate estimates of ca. 3 mm/day for juveniles are correct (M. R. Collins, unpubl. data), king mackerel spawned in early May could be recruited into the bycatch of the shrimp fishery in June. Late-spawned fish from the previous year may also be present at this time. In South Carolina, the open season for commercial trawling for penaeid shrimps in state waters usually extends from June through December, which coincides with the presence of juvenile mackerels in the heavily fished nearshore waters. In addition, mackerels were much more abundant in tows made in depths <9 m, which includes the preferred shrimping areas, than in deeper waters. This may be due either to greater abundance in these depths or to greater catchability in response to the fact that the trawl nets fish a larger portion of the water column in shallower areas.

It is difficult to accurately estimate the bycatch of mackerels in the commercial shrimp fishery owing to lack of current, detailed information from throughout the region on number of vessels, effort expended, gears used, and areas fished. However, our catch rates suggest that the impact of tongue nets on mackerel stocks may be significant. As the current status of these stocks is such that strong restrictions have been imposed on both the recreational and commercial fisheries, it is unfortunate that the situation may be exacerbated by a potentially large bycatch of juvenile mackerels in the shrimp fishery. More information is needed on the ecology and behavior of young mackerels, and their vulnerability to various gears, in order to resolve this conflict.

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STOMACH CONTENTS OF COMMERCIALLY CAUGHT HUDSON RIVER STRIPED BASS, *MORONE SAXATILIS*, 1973–75

The Hudson River estuary is a detritus-driven ecosystem. Only a few of the 100 or more reported fish species function as tertiary piscivores more typical of a grazing food chain. Of these few species, which include the American eel, *Anguilla rostrata*, and the summer-transient juvenile

12559, Charleston, SC 29412, pers. commun. May 1987.

bluefish, *Pomatomus saltatrix*, striped bass, *Morone saxatilis*, are probably the most important in terms of biomass and commercial value. However, commercial fishing for the American eel and striped bass has been banned in the Hudson since 1976 because both species are contaminated with higher levels of toxic polychlorinated biphenyls (PCB's) than most other Hudson River fish species.

To date, only one published paper has touched upon the diet of prespawning Hudson River striped bass larger than 400 mm TL (Gardinier and Hoff 1982), and their results for fish of that size are based on less than 10 samples for which fish remains were identified to species or family level. The present paper describes the findings of stomach content analysis for 510 striped bass, most of which were prespawning adults larger than 400 mm TL (Fig. 1) collected during the spring months of 1973–75 by commercial gill nets in the Tappan Zee region of the Hudson River.

Description of Sampling Area and Methods

The Tappan Zee gill-net fishery is located approximately 90 m south of the Tappan Zee Bridge at river km 43.5 (measured from the Manhattan Battery) in a relatively shallow section that is 4.5 km wide, a location through which many of the spawners move on the way to upstream spawning grounds. The staked gill nets were set perpendicularly to the north-south current in water depths of 2.4–9.8 m and spanned a distance of approximately 1.6 km out to the dredged channel on the east side of the river. Stretched mesh sizes were 11.4, 11.8, 12.1, 12.7, 13.3, and 14.0 cm. Water temperatures during the sampling period ranged from approximately 6° to 19.5°C, and the salinity was essentially that of freshwater, rarely rising above 300 mg/liter. Sampling dates included the following periods in each year: 28 March–9 May 1973, 8 April–20 May 1974, and 6 April–19 May 1975. Fish were collected from the nets at 8–12 h intervals, placed on ice, and taken directly to a laboratory for total length (TL) measurements and stomach content analysis. Prey items were identified with the aid of a binocular dissecting scope and frequency of occurrence was noted.

Results

Stomach Content Analysis

A summary table of stomach content data, pooled for the three years of analysis (Table 1), shows that adult, prespawning striped bass were highly piscivorous and that 89% of the stomachs containing identified food items contained fish and 21% contained invertebrate remains, primarily those of *Crangon* species. Clupeid species were the most prevalent fish, with blueback herring, *Alosa aestivalis*, predominating. Most of the clupeids were adult, prespawning herring, approximately 200 mm TL.

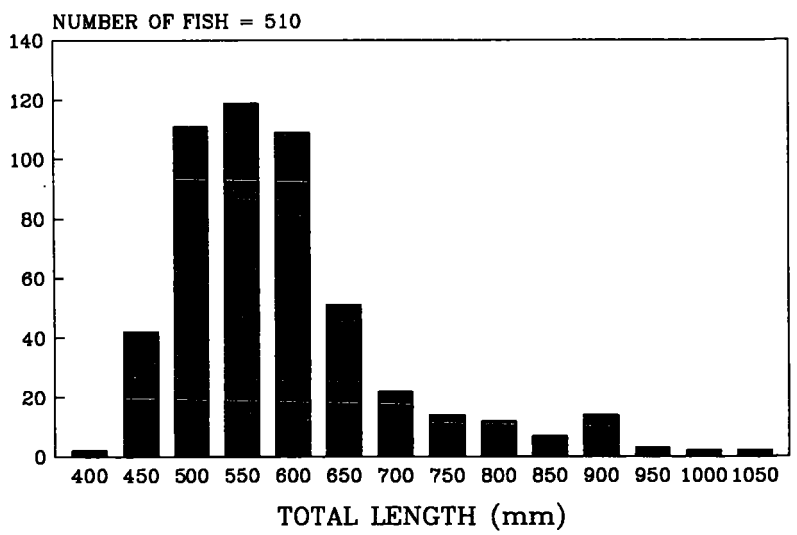

FIGURE 1.—Length distribution of Hudson River striped bass examined for stomach contents.

TABLE 1.—Stomach contents of adult prespawning striped bass collected by commercial gill net during spring 1973, 1974, and 1975.

Food item	Number of stomachs in which item occurred	% Frequency of occurrence based on total stomachs analyzed (n = 510)	% Frequency of occurrence based on number of stomachs containing identified food items (n = 201)
Fish	179	35.1	89.1
Clupeidae	73	14.3	36.3
Alosa pseudoharengus	13	2.5	6.5
Alosa aestivalis	29	5.7	14.4
Brevoortia tyrannus	3	0.6	1.5
Clupeidae	28	5.5	13.9
Morone spp.	9	1.8	4.5
Morone americana	6	1.2	3.0
Morone saxatilis[1]	1	0.2	0.5
Morone spp.	2	0.4	1.0
Other fish	29	5.7	14.4
Ammodytes americanus	14	2.7	7.0
Microgadus tomcod	7	1.4	3.5
Osmerus mordax	2	0.4	1.0
Syngnathus fuscus	2	0.4	1.0
Anchoa mitchilli	2	0.4	1.0
Ictalurus catus	1	0.2	0.5
Scomber scombrus	1	0.2	0.5
Unidentified fish remains	68	13.3	33.8
Invertebrates	43	8.4	21.4
Crangon spp.	38	7.5	18.9
Polychaeta	5	1.0	2.5
Unidentified contents	11	2.2	Not applicable
Total stomachs analyzed			510
Number (percent) containing identified food items			201 (39.4)
Number (percent) containing food material (identified and unidentified)			212 (41.6)
Number (percent) empty			296 (58.4)

[1]Two yearling striped bass in female collected 15 April 1974.

The next most abundant fish prey species in the composite 1973–75 sample was the American sand lance, *Ammodytes americanus*. Sand lance were present in striped bass stomachs only during 1975, when the frequency of occurrence was about 11% (Fig. 2). Atlantic tomcod, *Microgadus tomcod*, were found in striped bass stomachs only during 1973 when the frequency of occurrence was about 20%, somewhat higher than the frequency of clupeid species for that year (Fig. 2). These fish were yearling, postspawning Atlantic tomcod averaging about 125 mm TL. The *Morone* species, white perch, *M. americana*, and striped bass, had a frequency of occurrence of 4.5% for the composite sample and were present in striped bass stomachs every year (Fig. 2).

Discussion

Similar to findings in this study, Trent and Hassler (1966) found that blueback herring were predominant in the diet of adult, prespawning striped bass from the Roanoke River, NC, and Manooch (1973) found that herring ranked second after Atlantic menhaden, *Brevoortia tyrannus*, in the spring diet of adult striped bass from Albemarle Sound, NC. Data from Gardinier and Hoff (1982) do not indicate that blueback herring or clupeids were important in the diet of prespawning Hudson River striped bass collected during 1976 and 1977, but fish remains in bass stomachs were generally not identified to the family or species level in their study.

American sand lance are rarely found over muddy bottoms (Bigelow and Schroeder 1953; Leim and Scott 1966) or within estuaries (Massman 1960; Norcross et al. 1961), but they ranked second only to blueback herring in the diet of Hudson River striped bass. Sand lance were not reported from the Hudson River prior to 1975 when adults and larvae were relatively abundant in February–April ichthyoplankton collections south of the Tappan Zee Bridge (Dew and Hecht 1976). Data from the present study (Fig. 2) and from early spring ichthyoplankton sampling during 1976 (Dew, unpub. data), indicate that sand lance are not abundant every year in the Hudson, but it is probable that during some years adult sand lance serve as important alternate prey for prespawning striped bass.

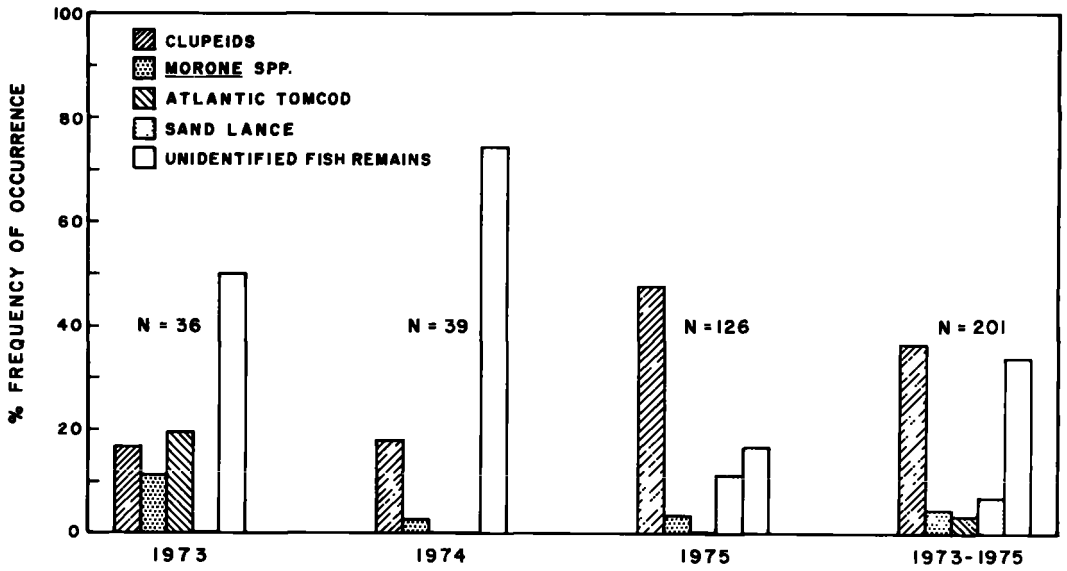

FIGURE 2.—Percent frequency of occurrence of fish prey categories based on number of stomachs containing identified food.

The fact that Atlantic tomcod were found only during 1973 may be due to a sampling artifact because 1973 was the only year in which March samples were taken, and all tomcod prey were found during March 1973. In March, gravid alewives, *Alosa pseudoharengus*, and blueback herring have not yet moved into the estuary and, prior to the arrival of these apparently preferred prey species, Atlantic tomcod may serve as an alternate forage fish. Thus the winter-spawning Atlantic tomcod may be a regular diet item at a time when alternate prey species are not available.

It is evident from Table 1 that there are several alternate fish prey for striped bass in the Hudson River (e.g., blueback herring, sand lance, alewife, Atlantic tomcod, white perch, and striped bass), and it is expected that striped bass predation upon these species would be of a compensatory nature. In a simple predator-prey situation where there are no alternate prey, predation is often depensatory (Neave 1953) because a population of predators would tend to seek out and consume a high proportion of small year classes and a lower proportion of strong year classes. In a more complex community where there are several species of prey, predation may be compensatory if predators change their feeding habits in response to the availability of food (Ivlev 1961; Forney 1971). That is, if several equally suitable prey species were available within a system, the predator species would tend to feed more heavily on the most abundant species, thus acting in a compensatory manner.

The ratio of white perch to striped bass in stomach samples identified to the species level is 6:1 (Table 1). This ratio is based on a small sample size, but it closely approximates the long-term average ratio of 5.9:1 for annual CPUE values for white perch and striped bass collected in several hundred bottom trawls from the Haverstraw Bay region (Milepoint 36) during 1971–77 (Lawler, Matusky and Skelly Engineers unpubl. data). In other words, yearling and older white perch and yearling striped bass may be equally attractive prey species, and their frequency of occurrence in adult striped bass stomachs may depend primarily upon the frequency of random encounters rather than active prey selection. If this were true, the frequency of cannibalism should be greatest during those years when the abundance of yearling striped bass relative to white perch (and other species) was greatest.

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ACCUMULATION OF AGE PIGMENTS (LIPOFUSCIN) IN TWO COLD-WATER FISHES

In fisheries management, age structured models are the preferred method for meeting the key objectives of estimating optimal yields and determining the effect of fishing on stock structure (Gulland 1978). However, few species of commercial marine fishes exist in which age can be determined with certainty (Boehlert 1985). The concentration of age pigments (lipofuscin) (Ettershank 1984) in fish tissues (Agius and Agbede 1984) may be a measure of fish age that could be used to validate other ageing techniques and might also improve estimates of age of long-lived species where other techniques are difficult to apply.

Lipofuscin originates in biological membranes through lipid peroxidation (Tappel 1975). Lipofuscin accumulation has been documented for a wide variety of animals, from mammals to the bread-mold *Neurospora* (Ettershank et al. 1983 and references therein). The rate of accumulation has been shown to be constant during the lifetime of laboratory-raised mice (Reichel 1968; Miquel et al. 1978), dogs (Munnell and Getty 1968), fleshflies (Ettershank et al. 1983); man (Strehler et al. 1959); and also wild populations of mice (Dapson et al. 1980). On the other hand, the rate of lipofuscin accumulation has been shown to vary with level of activity and lifespan (Sohal and Donato 1978). It is expected that the rate in which lipofuscin accumulates with age in a natural population of fishes, or stock, with its free genetic interchange and likely common habitat, would be fairly uniform (but see Smith 1987). In addition, if measurements are made in nonmitotic and constantly metabolizing tissues such as brain or myocardium, the variation in concentration due to environmental effects is least likely.

In this paper we present the results of a preliminary study designed to assess the usefulness of extracted lipofuscin as a method of ageing fishes. Two species of cold-water fishes are included: the rainbow trout, *Salmo gairdneri*, reared in captivity, and of known age; and the Dover sole, *Microstomus pacificus*, a long-lived fish, in which age is not known with certainty. We present spectral characteristics of the extracted lipofuscin from several tissues and the change in concentration of lipofuscin with fish age.

Materials and Methods

Specimens of Dover sole were collected on December 1986 off Point Conception. Ages were estimated by J. Butler, E. Lynn, and M. Drawbridge of the Southwest Fisheries Center using otolith sections. Ages ranged from 2.7 to 44.7 years (average of three readings). Specimens of the species *Salmo gairdneri* were collected in July 1986 at Hot Creek Hatchery. Ages ranged from 3 months to 3 years.

Samples were frozen after collection and kept at −80°C until analysis. Studies by Nicol (1987) showed that this form of preservation yielded the lowest fluorescence when compared with ethanol and formalin-preserved samples. There was no indication that the level of fluorescence changed as a function of time of preservation or by interaction with the extracted lipofuscin, as in the case for formalin. To excise the brain, the top of the skull was opened and the four brain lobes were removed as a unit, without the optic nerve. To excise the heart, we separated the muscle from connective tissue, blood vessels, and fat deposits.

Three methods were compared for maximum lipofuscin extraction. The first two methods (Tappel 1975; MacArthur and Sohal 1982) were specifically developed for lipofuscin extraction and employed chloroform:methanol (2:1) as the extractive solvent; they differ in the optimal volume-to-weight ratio (30:1 and 20:1, respectively), temperature of extraction, and number of times the chloroform phase is washed with water. The third method was developed for lipid extraction in fishes (Bligh and Dyer 1959) and uses chloroform:methanol:water (1:2:0.8) as the extractive solvent. Subsamples ($n = 3$) of cerebellum of *Stenella* sp. collected at the eastern tropical Pacific and kept at −30°C were defrosted, dried with lint-free paper, weighed, and extracted following the three methods as described originally.

Tissues from Dover sole were extracted basically following the MacArthur and Sohal (1982) technique, with two additional steps to ensure a complete washing out of flavoproteins and photooxidation of retinol when present (Fletcher et al. 1973). Tissue was freeze dried prior to analysis. Ten mL of chloroform:methanol (2:1, v/v) was added to a homogenizer containing the sample for a final solvent:sample ratio of about 120:1 (vol/dry weight). The sample was ground with a teflon pestle attached to an electric drill and later submerged in a 40°C water bath for 1 minute. A 2 mL subsample was taken from the homogenate. Three mL of deionized water was added, the sample was shaken, and the emulsion centrifuged 10 minutes at 1,912 *g* and 0°C. After centrifugation, the hyperphase was decanted and a second rinse performed. After decanting the hyperphase a second time, 1 mL of the hypophase (chloroform containing lipofuscin) was sampled and transferred to a polypropylene tube. Three mL of chloroform were added to the sample (for a total of 4 mL) which was then exposed to UV irradiation (254 nm) for 1–2 minutes to photooxidize retinol. This last step was routinely performed for liver tissue.

Samples were then transferred to glass tubes, sealed, and kept in the refrigerator until analysis. Sample fluorescence was measured at the emission peak (430–440 nm) in a quartz cuvette with a Perkin Elmer Fluorescence Spectrophotometer[1] Model MFP-44A. The sample was excited at the peak of fluorescence excitation (~360 nm). The intensity of the fluorescent emission (at 430 nm) was normalized to the intensity of the quinine solution standard (1 mg L^{-1} in 1N sulphuric acid) and expressed in fluorescence units.

Lipofuscin in Dover sole is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration, calculated by dividing the total lipofuscin content by the dry weight of the entire organ.

Lipofuscin from rainbow trout tissues was extracted following the Bligh and Dyer (1959) technique, without modifications. Whole tissues were ground in water with a tissue homogenizer to give a final concentration of 100 mg of tissue (wet weight) in 0.8 mL of homogenate. A sample of 0.8 mL was taken and solvents were added to give a final ratio of 1:2:0.8 (chloroform:methanol:water) with a solvent to sample ratio of 20:1 (vol/w). The sample was then filtered through a 2.4 cm glass fiber filter (Whatman GF/C), the tissue re-extracted with 1 mL of chloroform and refiltered. The extract was then washed with 3 mL of water, shaken, and centrifuged for 10 minutes at 1,912 *g* and 0°C. One mL of the chloroform hypophase was subsampled and fluorescence estimated as described above.

Lipofuscin in rainbow trout is expressed as 1) total lipofuscin content per organ and 2) weight-specific lipofuscin concentration (total lipofuscin content of the organ divided by its wet weight).

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

Results

Efficiency of Extraction

Lipofuscin was successfully extracted and quantified from three different fish tissues: brain, heart, and liver. Wavelengths of fluorescence excitation and emission maxima of extracted lipofuscin in chloroform are presented in Figure 1. All maxima are within the range cited by Sheldahl and Tappel (1973); fluorescence excitation maxima were between 340 and 370 nm and fluorescence emission maxima between 420 and 470 nm.

Retinol (wavelengths of maximum fluorescence excitation at 325–340 nm and maximum fluorescence emission at 475 nm) was photooxidized by exposing the chloroform extract to UV irradiation (254 nm). As expected, retinol was found in liver and sometimes it was present in brain and heart tissues. For example, wavelengths of fluorescence excitation and emission maxima in liver of Dover sole shifted from 352 to 365 nm and from 470 to 440 nm, respectively, after UV irradiation (see Figure 1C). Mullin and Brooks (1988) also found that this UV irradiation is effective in oxidizing retinol although they did not find significant retinol interference in fish tissue. It seems liver tissues may require UV irradiation to oxidize retinol while brain and heart tissue should be checked for retinol presence before irradiation.

The extractive efficiency of the three methods tested are compared in Table 1. All methods extracted similar fluorescent compounds from the brain of *Stenella* sp., as the fluorescence excitation and emission spectra were similar. The MacArthur and Sohal (1982) method extracted significantly more fluorescent pigment, than did either the Tappel (1975) or the Bligh and Dyer (1959) method which extracted 66% and 46% of maximum extraction, respectively). Thus all three methods are useful for quantitative estimation of extractable lipofuscin in fish tissue but

TABLE 1.—Comparison of the three methods of lipofuscin extraction in brain tissue. Fluorescence excitation at 360 nm and fluorescence emission at 440 nm. Results are presented as fluorescence units per mg of wet tissue, where the fluorescence emission signal is normalized to the intensity of emission of a standard quinine sulfate solution (1 mg L^{-1} in 1N sulphuric acid). The three methods were significantly different from each other, $P < 0.05$, Newman-Keuls range test (Zar 1974). ANOVA: F ratio = 21.81, 2 df, $P < 0.05$.

	Fluorescence units			Fluorescence maxima	
	Average 10–3	SD 10–3	n	Excitation (nm)	Emission (nm)
MacArthur and Sohal (1982)	4.30	0.39	3	362	445
Tappel (1975)	2.83	0.37	3	362	440
Bligh and Dyer (1959)	1.98	0.45	3	360	445

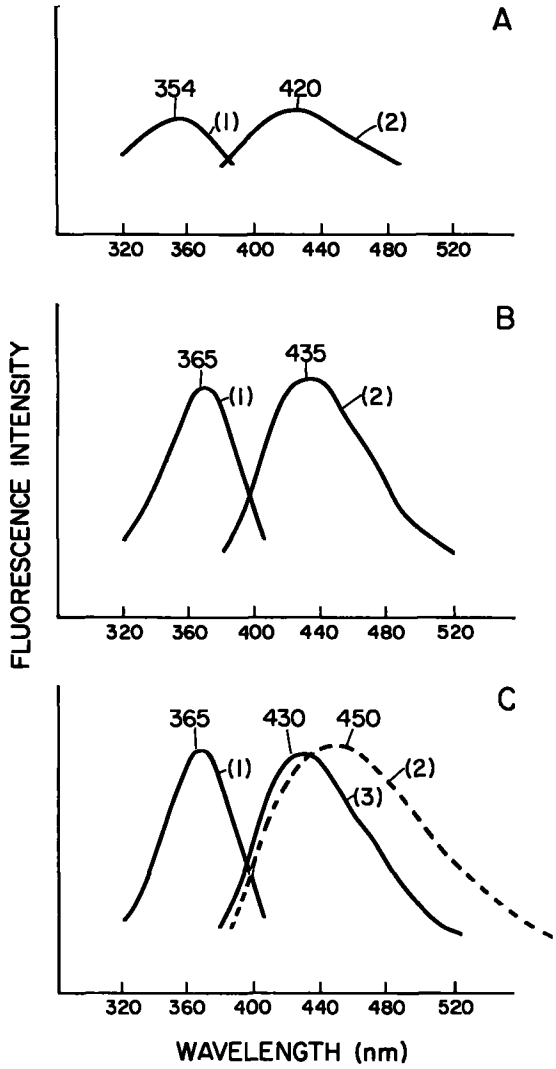

FIGURE 1.—Spectral characteristics of lipofuscin extracted from Dover sole, *Microstomus pacificus*, tissues (uncorrected spectra). In chloroform. (A) Brain: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 440 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (B) Heart: (1) Lipofuscin excitation spectrum (emission wavelength 430 nm); (2) lipofuscin fluorescence emission spectrum (excitation wavelength 365 nm). (C) Liver: (1) Lipofuscin fluorescence excitation spectrum (emission wavelength 430 nm); (2) lipofuscin emission spectrum (excitation wavelength 365 nm) before UV radiation; (3) Same as (2) after UV radiation (254 nm).

comparisons of amount of concentrations between tissues or species cannot be made if different extraction methods are used.

Lipofuscin Concentration

The total concentration of extracted lipofuscin in Dover sole brain tissue was positively correlated with fish length (Fig. 2A) ($Y = -15.4 + 0.516\,X$, $r^2 = 0.43$; $b \neq 0$, $P < 0.01$, $t = 5.1$, df = 34). Furthermore, total extracted lipofuscin content in the brain was positively correlated with age in organisms estimated by annular increments in otoliths to be from 2 to 15 years old (Fig. 3A) ($Y = -2.5 + 1.0\,X$, $r^2 = 0.75$; $b \neq 0$, $P < 0.01$, $t = 5.5$, df = 10). On the other hand, in older Dover sole (estimated age from 20 to 45 years; $n = 26$) the total extracted lipofuscin in the brain did not increase with their estimated age. The concentration of lipofuscin in the brain (extracted lipofuscin concentration per unit of g dry weight) followed a similar pattern (Fig. 3B). The concentration in the brain increased linearly with age for fish 2–15 years old ($Y = 30.39 + 14.85\,X$, $r^2 = 0.79$, $b \neq 0$, $P < 0.01$, $t = 6.66$, df = 10) but fishes older than 15 years did not show an increase in pigment concentration with age.

The total extracted lipofuscin content extracted from rainbow trout brains increased with age (Fig. 4A) ($Y = 0.14 + 0.18\,X$, $r^2 = 0.37$; $b \neq 0$, $P < 0.01$, $t = 3.75$, df = 23), as did the content of the heart (Fig. 4C) ($Y = -0.54 + 0.82\,X$, $r^2 = 0.67$; $b \neq 0$, $P < 0.01$, $t = 7.36$, df = 23), and liver (Fig. 4E) ($Y = -2.86 + 5.81\,X$, $r^2 = 0.62$; $b \neq 0$, $P < 0.01$, $t = 7.54$, df = 34) from 3 months to 3 years. The concentration of extracted lipofuscin per unit wet weight of heart tissue did not change with age (Fig. 4D) whereas that of brain and liver tissue decreased with age (Fig. 4B, F).

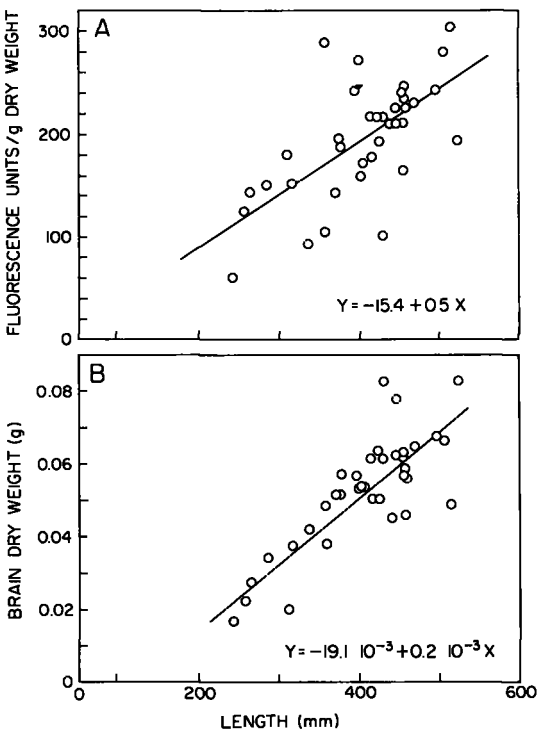

FIGURE 2.—Dover sole, *Microstomus pacificus*, brain: (A) Extracted lipofuscin per unit of dry weight as a function of fish length (mm) (n = 36); (B) brain dry weight (g) as a function of fish length (mm). Fluorescence units: the intensity of fluorescence normalized to a standard solution of quinine sulfate (1 mg L^{-1} in 1N sulphuric acid).

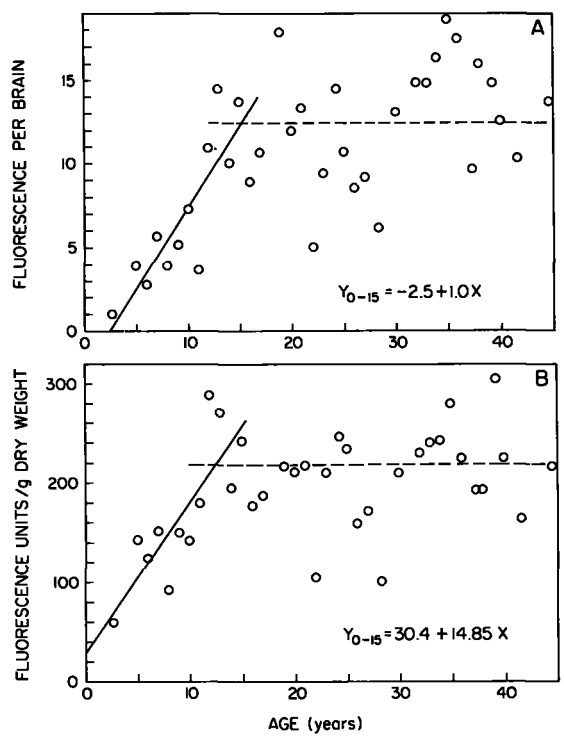

FIGURE 3.—Lipofuscin in Dover sole, *Microstomus pacificus*, brain tissue as a function of age ($n = 36$). (A) Total lipofuscin content per brain; (B) weight-specific (g dry weight) lipofuscin in brain.

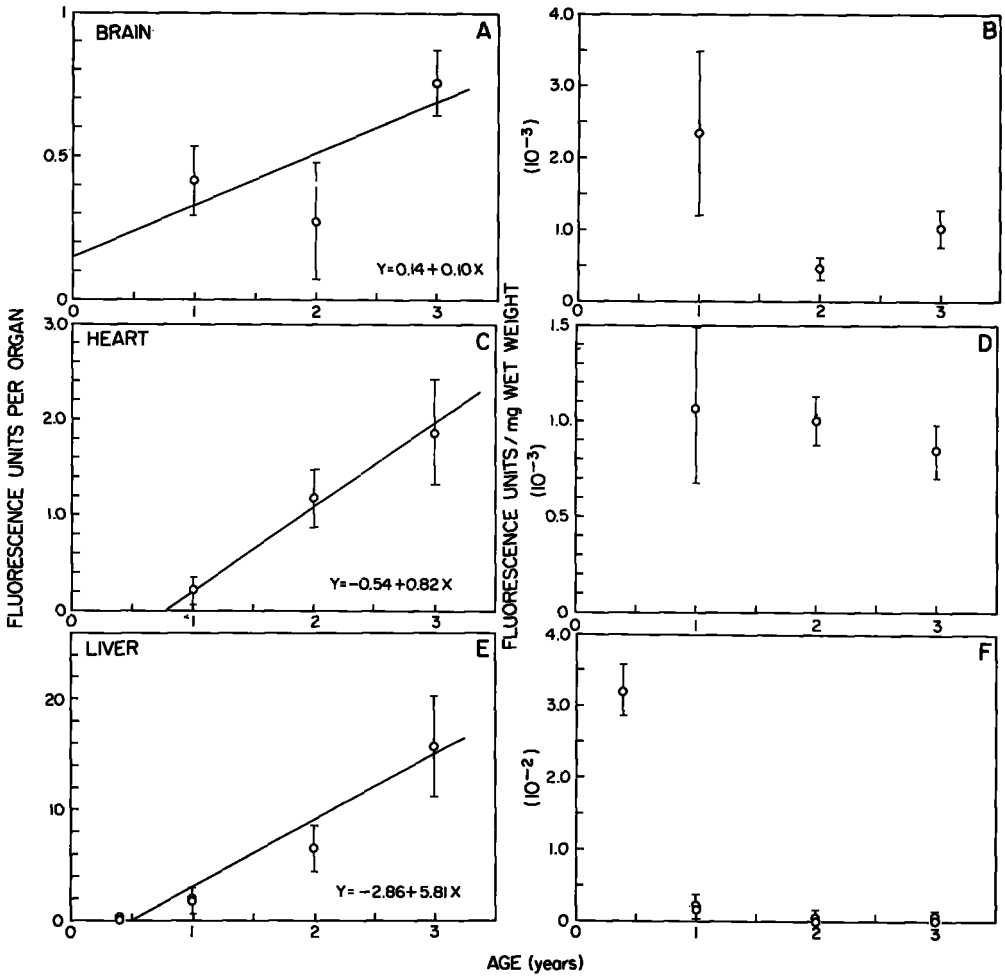

FIGURE 4.—Lipofuscin in rainbow trout, *Salmo gairdneri*, as a function of age ($n = 21$). (A) Total lipofuscin in brain; (B) weight-specific (mg wet weight) lipofuscin in brain; (C) total lipofuscin in heart; (D) weight-specific (mg wet weight) lipofuscin in heart; (E) total lipofuscin in liver; (F) weight-specific (mg wet weight) lipofuscin in liver.

Discussion

Our results indicate that lipofuscin accumulated in the brain of Dover sole with time (Fig. 2A). The concentration of lipofuscin increased over a wide range of fish lengths and with estimated age of 15 years but did not increase with older fish. Several explanations exist for the lack of change in concentration in older fish: 1) older fish were incorrectly aged; 2) growth of brain tissue masked the actual rate of accumulation; and 3) the rate of accumulation changed during the lifespan of this species due to changes in metabolic activity. Either one or several of these factors may cause the lack of lipofuscin accumulation in older fish. We consider each of these issues below.

We do not know the accuracy of the age determination in Dover sole but believe it is unlikely that 3 readers would confuse fish aged 30–40 years with those of 20 years. Although future research will shed more light on this controversial subject, we think that grossly inaccurate age determination is the least likely an explanation.

A key difference between fishes and other organisms in which lipofuscin accumulation has been clearly documented as a function of chronological age (mammals and invertebrates) is that

fishes have indeterminate growth. For example, Figure 3B indicates that the brain of Dover sole continues to grow long after this fish begins reproduction (450 mm). Thus, unlike mammals and invertebrates which have determinate growth, the total content of extractable lipofuscin in any fish organ cannot be used as a measure of age but rather concentration (content per unit of weight) must be used. Furthermore, even the concentration of lipofuscin in the brain, a slow growing tissue, is a function of both the rate of lipofuscin accumulation and the rate of tissue growth. It follows then, that if the rate of brain growth is such that it masks the actual rate of lipofuscin accumulation in older organisms, lipofuscin concentration will not increase with time.

A critical assumption underlying the use of lipofuscin as a determinant of age is that metabolic rate, and hence lipofuscin accumulation rate, remains fairly constant over the portion of the life history of interest. The rainbow trout were reared in a hatchery where no net change in the environment occurred from 1983 to 1985. Dover sole, on the other hand, gradually migrate into deeper, colder, and less oxygenated waters as they age. Presumably the metabolism of fish under these conditions would be lower as might be the rate of lipofuscin accumulation in the brain.

The literature on fishes provide no conclusive evidence that lipofuscin is an accurate index of age over the entire lifespan. Hill and Radtke (in press) reported that the extracted lipofuscin per unit dry weight in the brain of the tropical fish *Dascillus albisella* accumulates exponentially with age. The relationship is driven by a single point for an 11-year-old individual and it would probably be linear without that single point, if only fish 1–7 years old were considered. In hatchery-reared *Cyprinus carpio* the total extracted lipofuscin per unit of dry weight in the brain of fish of the same age (6 years) increased with weight over 8-fold range in weight (Griven et al.[2]). About 45% of the lipofuscin content could be explained by difference in weight among fish. Thus, in fish of the same age there was a strong size effect on lipofuscin concentration. These results are very similar to those found in this study. Aloj Totaro et al. (1985) found that lipofuscin increased over a range of 0–2 years. But the method was different as they measured lipofuscin granules present in the electric lobe of *Torpedo marmorata* brains rather than using extractable lipofuscin of the entire brain. Thus, all studies to date seem to indicate that accumulation occurs in the brains of fishes, but results are not conclusive owing to small sample sizes, limited age ranges, and failure to identify the effects of brain growth on rates of accumulation.

Additional research is required to evaluate lipofuscin as a method of age determination in fishes. The effect of brain growth on lipofuscin accumulation rates must be considered in such studies. A promising approach in this regard may be to estimate lipofuscin on a per cell basis instead of on a weight basis. This could be accomplished by either expressing extracted lipofuscin relative to DNA concentration or by histological techniques.

[2]Girven, R. J., R. W. Gauldie, Z. Czochanska, A. D. Woolhouse. Manuscr. in prep. A critical tests of the lipofuscin technique of age estimation in fish.

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EXTRACTABLE LIPOFUSCIN IN LARVAL MARINE FISH

The "age pigment", lipofuscin, is thought to be a biochemically heterogeneous byproduct of the peroxidation of polyunsaturated lipids which accumulates in dense, intracellular inclusions called ceroid bodies. The material has been studied both microscopically and biochemically in tissues of several species (Miquel et al. 1977; Shimasaki et al. 1980; Dowson 1982), and some portion of it is quantitatively extractable with organic solvents (Fletcher et al. 1973).

Flies prevented from flying by putting baffles in the bottles in which they were raised, accumulated lipofuscin (as assessed by solvent extraction) more slowly than did free-flying flies but had a longer lifespan, so that at the ends of the respective lifespans the body contents of lipofuscin were similar in the two groups (Sohal and Donato 1978). Extractable lipofuscin thus appears to accumulate as a function of cumulative oxidative metabolism; it could be an indicator of physiological (rather than strictly chronological) age.

Additionally, if lipofuscin represents an integral of oxidative metabolism since birth and weight represents an integral of growth over the same period, the ratio of lipofuscin to organic weight should be proportional to the reciprocal of cumulative net growth efficiency [K_2 = growth/assimilation = growth/(growth + respiration), hence $1/K_2 = 1$ + respiration/growth].

Ettershank (1984a) introduced the fluorometric measurement of extractable lipofuscin as a measure of physiological age in growing marine crustaceans, based on the work with insects, and (1984b) recommended a simple method for routine use in marine work. He also argued (without presenting extensive evidence) that preservation

of tissue in formalin-seawater did not invalidate the analysis; thus, historical samples of zooplankton (and, presumably, larval fish) appeared to be usable for study of intraspecific geographic or interannual variability.

Although most studies of lipofuscin (especially by histology) have concerned postmitotic cells, such as nervous tissue, we evaluated the assay as an estimate of the relative efficiency of growth of larvae analyzed whole. That is, we were less interested in lipofuscin as an indicator of age (for which, as we show, other measures of mass are useful) than as an indicator of health whose relation to mass would reflect environmental conditions over time. We therefore investigated the importance of interfering fluorescing pigments (Csallany and Ayaz 1976), tested the effect of preservation in formalin (Nicol 1987), and measured the accumulation of extractable lipofuscin in three species of larval fish reared in the laboratory—California grunion, *Leuresthes tenuis*; white seabass, *Atractoscion nobilis*; and California halibut, *Paralichthys californicus* (hereafter referred as grunion, seabass, and halibut respectively).

Analytical Considerations

We analyzed lipofuscin by a method first described by Fletcher et al. (1973), as modified by Ettershank (1984b). The tissue to be analyzed (usually whole larvae) was frozen (−15° or −70°C) and later freeze-dried, and a 1–5 mg sample was homogenized in at least 2 mL of 2:1 chloroform:methanol in a Wheaton glass tissue homogenizer. After extracting for 3–4 hours at 4°C, 100 mM $MgCl_2$ (25% of the solvent volume) was added, and the solutions were thoroughly mixed and then centrifuged for 20 minutes at 3000 rpm at −4°C. The lower, chloroform layer was withdrawn for fluorometric analysis after reaching 20°C in a water bath, and the fluorescence was measured on a Turner 111[1] fluorometer using a CS 7–60 filter (approximately 360 nm) for excitation and a CS 47B filter (approximately 430 nm) for emission. A known concentration of quinine sulfate was the standard, and results are therefore reported as "fluorescence units" or FU/mg.

A stock solution of quinine sulfate (2 mg/L in 1 N H_2SO_4) was stored in a light-tight reagent bottle. To compare analyses done at different times, sets of standards were prepared from this stock in distilled water (0.02, 0.04, 0.06, 0.08, and 0.10 μg/mL). Some of the sets prepared over a year's time are shown in Figure 1; the overall reproducibility is good.

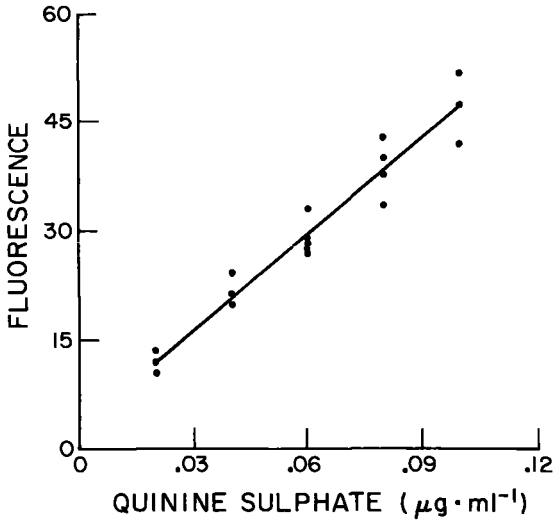


FIGURE 1.—Reproducibility of different sets of quinine sulfate standards prepared from a stock solution over a year.

Precision of the method, including extraction from tissue, was estimated by comparing replicate samples of liver and white muscle from adult halibut. The coefficients of variation for 5 determinations on each of 3 sets of tissue were for muscle, 0.2, 0.35, and 0.57, and for liver, 0.1, 0.15, and 0.18. The difference in variability between the two kinds of tissues is probably due to the greater difficulty in homogenizing muscle tissue.

Quinine sulfate standards were compared on a Farrand Spectrofluorometer, with excitation at 350 nm and emission at 420 nm, and on the Turner 111 fluorometer. The correlation coefficient for measurements on the two instruments was 0.97. We therefore used the Turner 111 routinely, so that analyses could be done easily in a hood.

Csallany and Ayaz (1976) described interference by retinol in the analysis of organic-solvent-soluble lipofuscin in mammalian tissues, and recommended a chromatographic step to remove this contaminant. We extracted a variety of fish tissues in 2:1 chloroform:methanol, and after addition of $MgCl_2$ and centrifugation, dried the chlo-

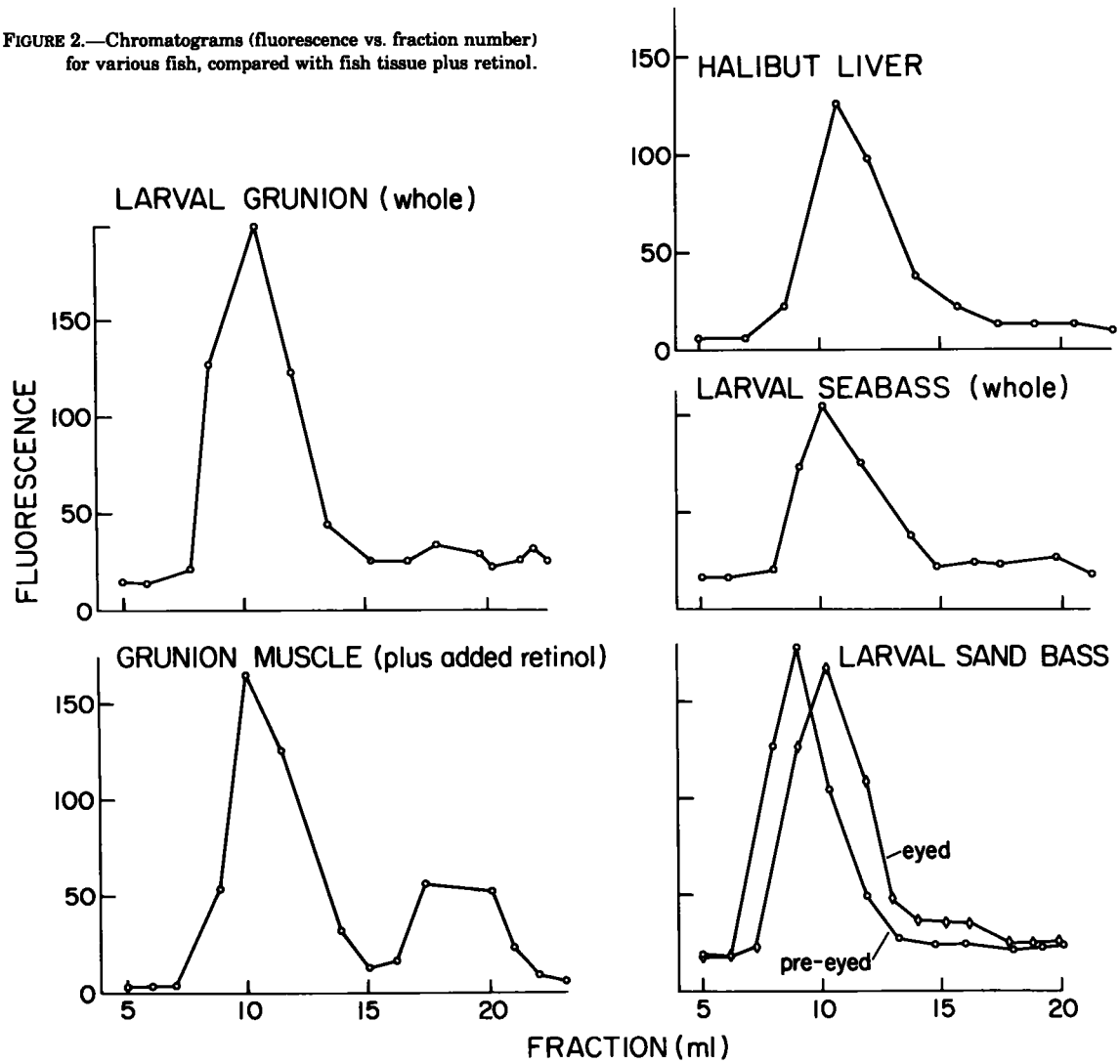
[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

roform layer gently (35°C) in an open vial overnight in a hood on a sand bath. The dried extract was reconstituted with 1:9 chloroform:methanol and chromatographed on a 30 cm Sephadex LH20 column at a flow rate of 3–4 mL/hour. A fraction was collected by hand every 20 minutes, its volume measured, and its fluorescence determined on the Turner 111 at the same wavelengths used for routine analysis of lipofuscin. To determine where a retinol peak would appear, we chromatographed a tissue extract to which a commercial preparation (Sigma) of retinol had been added. Also, extracts of larval fish in the pre-eyed stage were compared with extracts of larvae that had pigmented eyes, assuming that the eyed larvae would have more retinol.

A UV irradiation step had been proposed to degrade retinol where it may interfere with measurement of extracted lipofuscin, but Csallany and Ayaz (1976) reported that this procedure was ineffective. We therefore determined the time course of degradation of commercial retinol in 1:9 chloroform:methanol by UV irradiation in quartz tubes.

At the wavelengths we used, retinol was not an important interfering substance in a variety of larval fish and in the adult grunion muscle and adult halibut liver tissues (Fig. 2). There also was little difference between extracts of eyed and pre-

FIGURE 2.—Chromatograms (fluorescence vs. fraction number) for various fish, compared with fish tissue plus retinol.



eyed larvae. We therefore did not use UV irradiation routinely. If UV irradiation is used to degrade retinol, the exposure must be kept short (1 or 2 minutes), or else another compound fluorescing at these wavelengths appears (Fig. 3), giving the spurious impression that UV did not affect retinol; this may explain the negative results of Csallany and Ayaz (1976).

To evaluate the effect of preservation in formalin, we froze subsamples from stocks of larvae, and preserved other subsamples in 10% formalin in a glass container, using formalin from a glass reagent bottle. We analyzed frozen and preserved larvae after 3 months, and after an additional year we analyzed more preserved larvae.

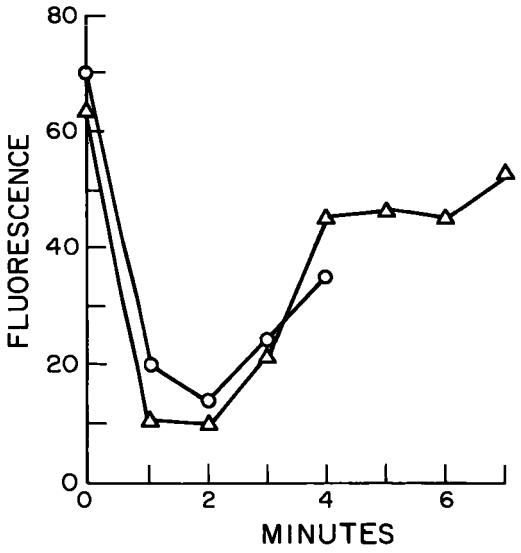


FIGURE 3.—Time course of fluorescence resulting from UV irradiation of duplicate batches (two symbols) of retinol.

Nicol (1987) recently demonstrated that formalin preservation significantly increases the fluorescence of lipofuscin extracted in chloroform-methanol, and our results show similar analytical problems (Table 1). There was significant enhancement in fluorescence in the larvae preserved for over a year, when compared with those preserved for 3 months. Quinine sulfate standards run at the same time as the samples for different periods were very similar (Fig. 4), indicating real changes with time of preservation. Thus, this method will not permit using historical collections of formalin-preserved animals to determine their relative physiological states until more is known about the time course and nature of the effect of formalin on the extract of preserved tissue.

Larval Growth Experiments

Seabass larvae were obtained from Hubbs Research Institute and halibut larvae from the Los Angeles County Natural History Museum; larval grunion were obtained by stripping adults and bringing fertilized eggs into the laboratory for hatching in an aerated, 10 L container of seawater at room temperature.

Larval grunion were reared in 40 L Nalgene tubs with spigots at the bottom (which facilitated emptying and cleaning), initially stocked with 100–120 newly hatched grunion per tub, with replicated "high" and "low" food concentrations. Larvae were fed newly hatched *Artemia* nauplii and the rotifer, *Brachionus*, which was cultured on *Dunaliella tertiolecta* in 100 L, lighted

TABLE 1.—Lipofuscin (as fluorescence units, FU) per animal and per unit dry weight (DW) of frozen vs. formalin-preserved larval fish. N = number of larvae per analysis.

	Frozen (3 months)		Preserved (3 months)		Preserved (1 year)	
	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$	FU (larva)$^{-1}$	FU (mg DW)$^{-1}$
Grunion	16.0	47.4	24.3	60.1	44.3	98.1
N = 15	16.7	47.3	31.0	76.7	45.0	93.1
	17.3	47.7	23.6	60.4	48.0	100.1
	17.0	49.7	24.0	63.0	54.3	112.7
			26.0	65.3	51.0	106.2
$\bar{X}$ =	16.8	48.0	25.7	65.3	48.5	102.0
Seabass	0.68	18.6	0.82	13.6	1.72	22.3
N = 30	0.47	13.0	0.71	12.0	2.05	26.3
	0.50	14.5	0.46	8.0	2.03	27.2
	0.43	12.7	0.52	8.7	1.63	22.2
	0.33	9.4	0.60	10.5	2.05	28.9
$\bar{X}$ =	0.48	13.6	0.62	10.6	1.89	25.4

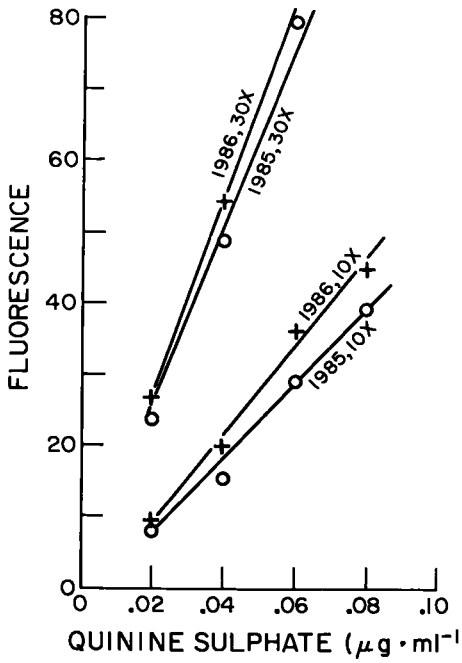


FIGURE 4.—Fluorescence of various concentrations of quinine sulfate standards read at 10× gain (lower pair of lines) and 30× gain (upper pair) in 1985 (lower line of each pair) and 1986 (upper of each pair).

polyethylene tubs augmented with f/2 phytoplankton nutrients (May 1971; Theilacker and McMaster 1971). One spring and one summer experiment were completed at ambient temperatures (spring = 17.5°–19°C, summer = 21°–23°C), with one of the "high food" containers in the second experiment kept at 26°C with an aquarium immersion heater.

We were unable to maintain absolute high and low food concentrations because of oscillations in the supply of food organisms. Thus, the high concentration was kept at 3 times the low concentration, although absolute amounts varied. The mean initial food concentrations in the spring experiment were 50 μg C/L (= "low") and 154 μg C/L (= "high"); in summer, 122 and 394 μg C/L, respectively. Tubs were censused every 2 days through each experiment to determine how much food was uneaten and how many larval fish had died (estimated by counting and removing corpses), and to add fresh food. In the low food containers, it was not unusual to find little uneaten food, particularly as the larvae grew. Once a week the tubs were emptied and the remaining larvae counted directly. It was clear from this direct census that all dead larvae were not accounted for by searching for corpses every 2 days because of cannibalism, necrophagy, or decay. Every 4 days a known number of larvae was removed; their lengths were measured and they were frozen for future analyses.

We could not estimate larval ingestion precisely because of the uncertainty in how many fish were alive through a 2-d interval. This problem was exacerbated as the larvae within each tub diverged in size, so that variance in individual ingestion increased. Although 3 times more food was offered in the high food containers, these larvae actually ingested about twice the amount of food as did those in the low food containers (Table 2). This difference was due to better survival in the high food containers, which affected the ratio between available ration and number of larvae. To compensate for this, we routinely harvested more animals from the high food containers than from the low food containers.

Freeze-dried animals or tissues were weighed on a Cahn electrobalance. Protein was determined by a method of Dorsey et al. (1977) on an aliquot of tissue homogenized in cold 1 M NaCl. DNA was measured by an ethidium bromide technique (Bentle et al. 1981, as modified by M. S. Lowrey). Basic measures of size—dry weight, protein, and DNA—were strongly and linearly correlated (Fig. 5), so that comparing lipofuscin with any of these measures would give similar patterns.

Lipofuscin accumulated as the larval fish grew (Fig. 6), but at quite different rates for the 3 species, grunion accumulating most rapidly (relative to gain in weight) and seabass much the slowest.

TABLE 2.—Estimated average ingestion, size, composition, and growth efficiency for 20-day-old, laboratory-reared larval California grunion. Compare with Figure 5.

	Spring experiment		Summer experiment	
	Low food	High food	Low food	High food
μg C ingested[1] per individual	701	1,723	1,379	2,792
μg dry weight per individual	755	1,305	901	1,895
μg DNA per mg protein	84.8	59.4	48.1	31.3
μg C[2] per individual	245	603	482	977
Growth from hatching (μg C)	104	462	341	836
Gross growth efficiency	15%	27%	25%	30%

[1]Calculated from measured carbon in *Brachionus* and *Artemia*.
[2]Estimated from literature values.

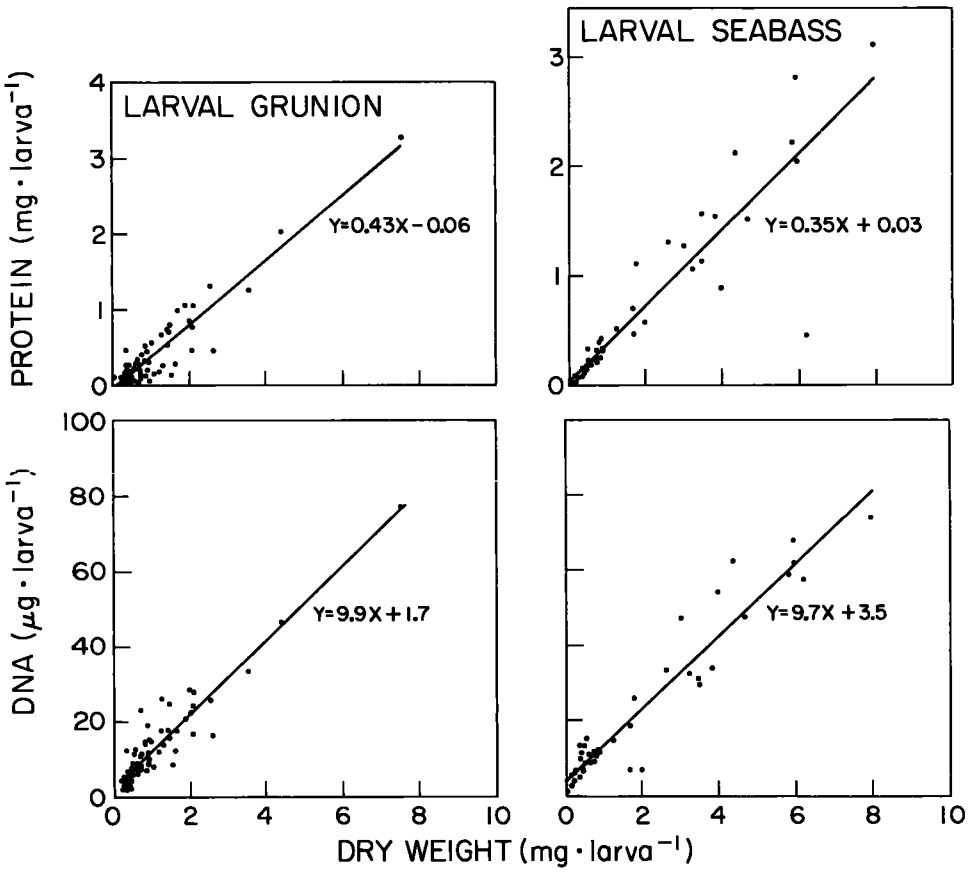


FIGURE 5.—Relations of protein (upper) and DNA (lower) to dry weight for laboratory-reared larval grunion (left) and white seabass (right).

This may reflect differences in the lifespans and metabolic rates; grunion are small fish, reaching maturity in a year and living less than 5 years (Frey 1971), while seabass and halibut grow to very much larger size and can live more than 20 years (Frey 1971; Thomas 1968).

Figure 7 shows the variability in the amount of lipofuscin in larvae of the same age. At time "0", all fish were newly hatched. The variance was low in the first few days, but increased dramatically with time because larvae within each tub grew (and, presumably, respired) at very different rates. There were differences in averages between high food and low food conditions, and between experiments (Table 2), but the variance in dry weight, protein, DNA, or lipofuscin was so large that the overlap obscured any differences between conditions of rearing.

Grunion and halibut larvae start life with greater concentrations of lipofuscin than do seabass, and though the concentration decreases rapidly as grunion and halibut age (Fig. 8), they still have almost a 10-fold greater concentration than do larval seabass when all are 20 days old. All three species increased in weight faster than they increased in lipofuscin, so the concentration of lipofuscin was "diluted" by growth. Because protein was a constant fraction of dry weight (Fig. 5, upper), this dilution was not due to skeletal growth alone. If the rate of weight-specific growth exceeds the rate of weight-specific respiration during early life, the concentration of lipofuscin should decrease, as observed, and only when growth ceases or slows considerably should lipofuscin accumulate relative to weight. Alternatively, lipofuscin could change chemically with time, becoming more difficult to extract (Vernet et al. 1988), so that the rate of accumulation of lipofuscin would be underestimated.

We attempted to stop growth by starving the

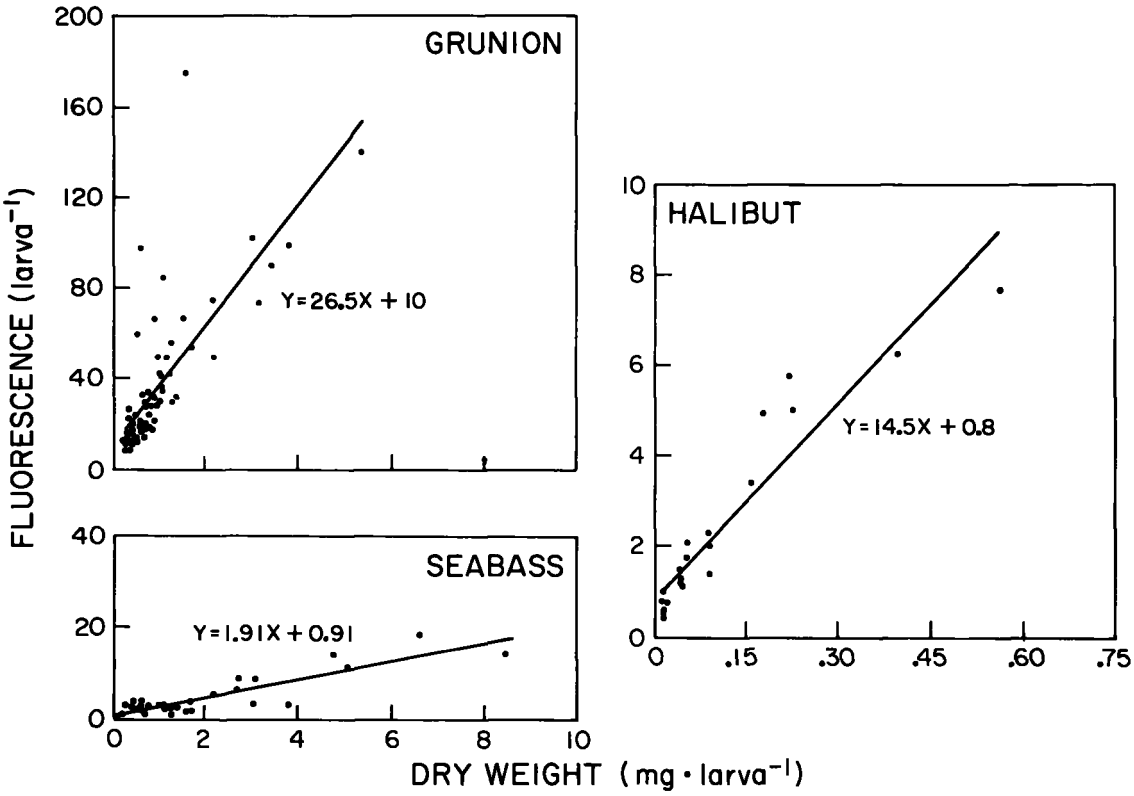


FIGURE 6.—Relation of lipofuscin fluorescence per larva to dry weight for larval grunion (upper left) white seabass (lower left), and California halibut (right). Note different axes.

larvae to see if we could detect an increase in lipofuscin. Table 3 shows results for seabass starved for the final 20% of the rearing period; there was no significant change in the concentration of lipofuscin. This is not what one would expect if accumulation of lipofuscin is proportional to physiological age, unless no lipid is metabolized during starvation. However, this result also could reflect slow transformation of lipofuscin from a more to a less soluble pool (Vernet et al. 1988).

TABLE 3.—Lipofuscin fluorescence (FU) per unit dry weight of larval white seabass starved for various periods after age 29 days. *N* = number of analyses; ranges in parentheses.

	FU (mg dry weight)$^{-1}$	*N*
Initial		
29 days old	2.4 (1.6–3.0)	4
Starved		
2 days	3.1 (2.3–4.0)	2
4 days	1.3 (0.54–1.7)	6
6 days	1.8 (1.4–2.3)	2
8 days	2.5	1

Conclusions

Our intent was to evaluate the utility of measuring extracted lipofuscin fluorometrically as an indicator of the integrated metabolic health of fish, especially preserved ones, and of relative net efficiency of growth. We conclude that this technique is unlikely to be useful in these ways, at least within the larval period. Although the accumulation of total body burden of lipofuscin was demonstrated, the variability among individuals grown under the same conditions became so large over time that we were unable to calibrate the method in an ecologically meaningful sense. The variability was evident in all measures of growth,

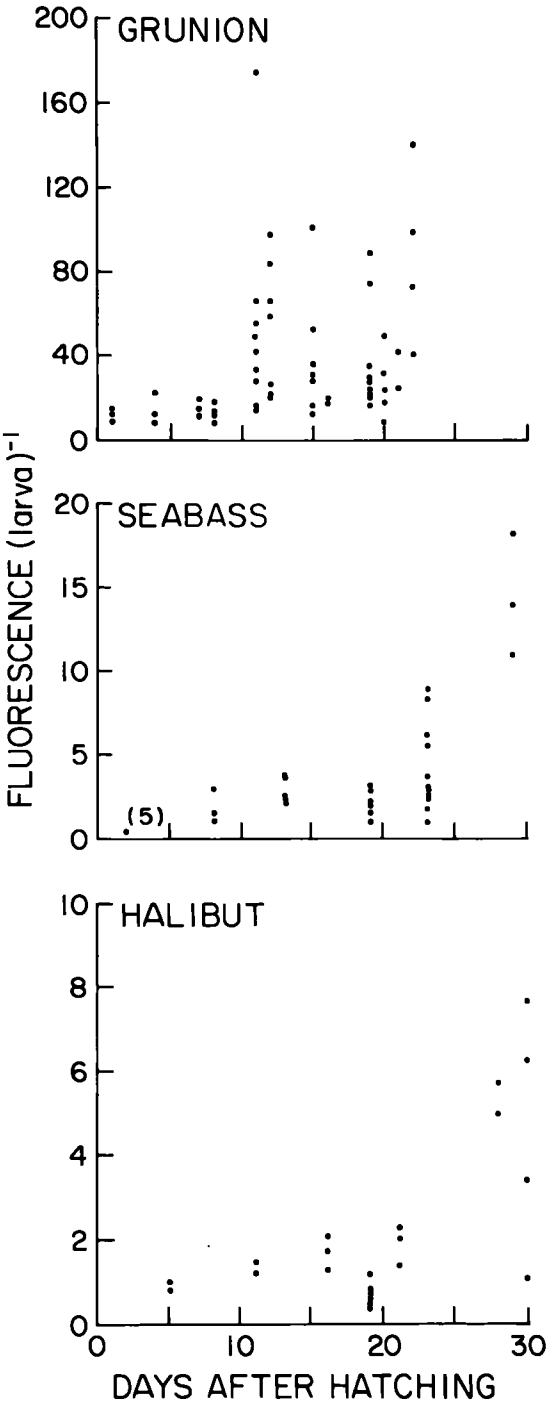


FIGURE 7.—Lipofuscin fluorescence per larva vs. age since hatching for laboratory-raised larval grunion (top), white seabass (center), and California halibut (bottom).

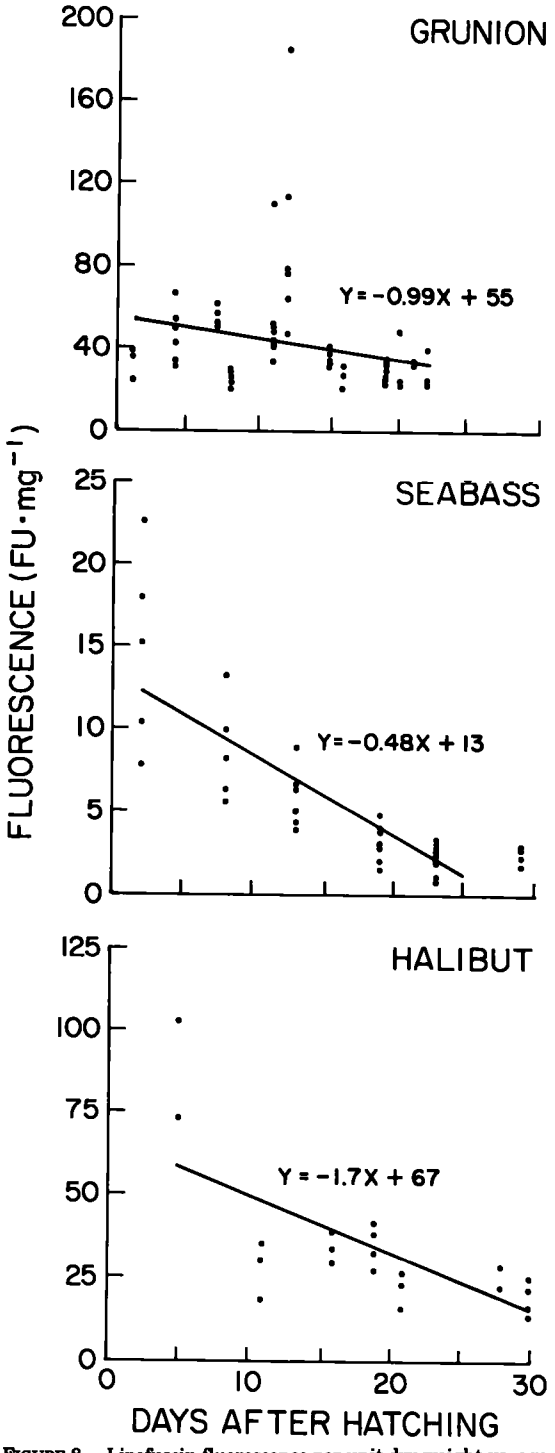


FIGURE 8.—Lipofuscin fluorescence per unit dry weight vs. age since hatching for laboratory-reared larval grunion (top), white seabass (center), and California halibut (bottom). Linear fits are for comparative purposes only; relations for seabass and halibut look curvilinear.

and is common in culture of larval fishes. Such variability may be reduced in nature, where runts may be subject to intense predation.

Lipofuscin analysis may be useful only when applied to postmitotic tissue, such as nervous tissue in mature fish, or to whole organisms whose mitotic growth has essentially ceased, such as adult copepods or insects (since the methods appear useful in arthropods—Ettershank et al. 1983; Sohal and Donato 1978). In these organisms, the vagaries of growth are reduced, and the accumulation of lipofuscin during starvation or exercise might show that lipofuscin concentration is interpretable as a measure of physiological age, habitat quality, and net growth efficiency.

Lipofuscin is known to be a polytypic substance, probably variable in composition among different organisms. We have assumed that a constant proportion of the same substance is extracted. This may not be true (Vernet et al. 1988), and considerable work remains to be done on the basic biochemistry of the component substance(s). Though the extraction and fluorometric measurement is tantalizingly simple, it may well be that the microscopical method used to quantify "ceroid bodies" is the best approach. Fluorescent techniques used in histochemical research (Brizzee and Jirge 1981), combined with automatic imaging procedures, might decrease the tedium of staining and visual microscopy.

Acknowledgments

We thank Refik Orhun and Steve Cadell for the larval white seabass and halibut, and Maria Vernet and two referees for helpful comments. Research was supported by California Department of Fish and Game project C-921 and National Science Foundation grant OCE86-00742.

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NOTICES

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ERRATA

Fishery Bulletin: Vol. 86, NO. 1

Butler, John L., and Darlene Pickett, "Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*," p. 163–167.

Pages 165 and 166 have incorrect figures for the legends, please replace with the following:

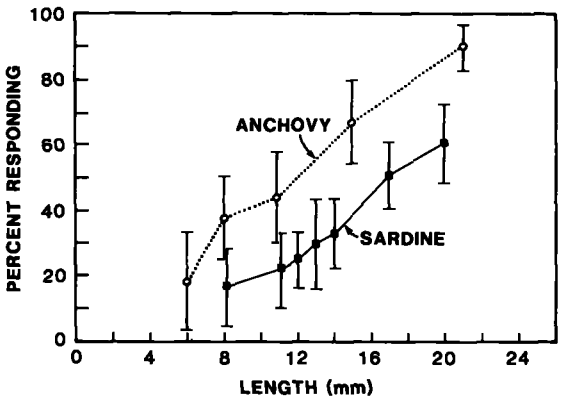


FIGURE 1.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).

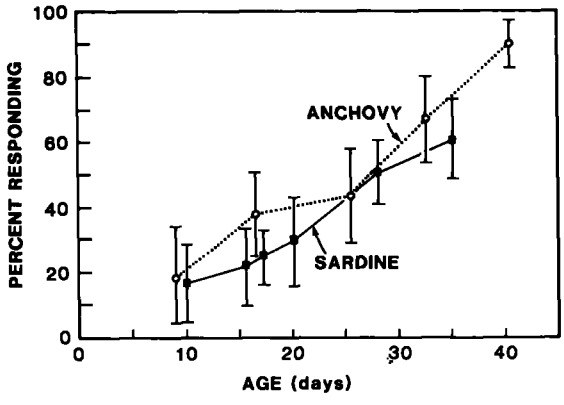


FIGURE 2.—Increase by age of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, responding to attack by adult northern anchovy and 95% confidence intervals. Size categories of reared larvae have been converted to ages using growth rates estimated from the field. Data on anchovy larvae from Folkvord and Hunter (1986).

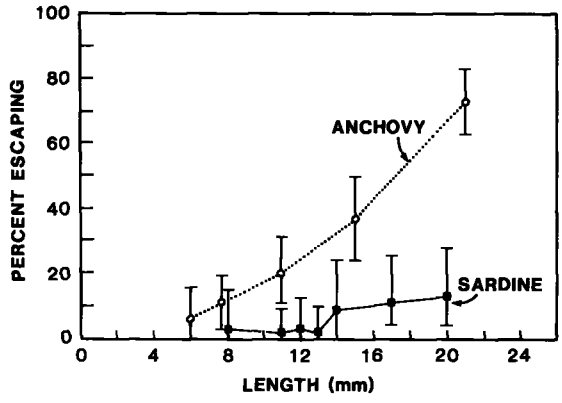
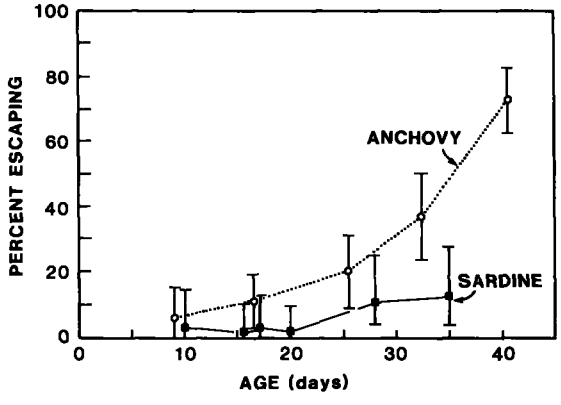


FIGURE 3.—Increase by size of the percentage of Pacific sardine larvae, *Sardinops sagax*, and northern anchovy larvae, *Engraulis mordax*, escaping attack by adult northern anchovy and 95% confidence intervals. Data on anchovy larvae from Folkvord and Hunter (1986).



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HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: I. SHIP SURVEYS

JAY BARLOW[1]

ABSTRACT

The density and total population size of harbor porpoise along the coasts of California, Oregon, and Washington are estimated from ship surveys using line transect methods. Surveys were completed between September 1984 and May 1986 using teams of 3–5 observers. Data include 852 porpoise groups sighted during 6,590 km of transects. Sighting rates varied more due to effects of sea state than due to the presence of rain, fog, or sun glare. Experiments using additional observers indicate that approximately 22% of trackline groups were missed by a team of 5 observers. Harbor porpoise density is calculated from transects along the 18 m isobath and is extrapolated to other depth zones based on a model of porpoise abundance as a function of depth. Total population size is estimated as 45,713 (SE = 7,865) animals.

Approximately 200–300 harbor porpoise are taken annually in central California set net fisheries (Diamond and Hanan[2]; Hanan, et al.[3]). Little is known about porpoise abundance in this area. Dohl et al.[4] estimated that 1,600–3,000 porpoise reside in central and northern California based on their aerial surveys of coastal cetaceans. However, because harbor porpoise are frequently missed in aerial surveys (Kraus et al. 1983), this estimate is probably low. More information is needed on abundance, distribution, and population structure to determine the significance of harbor porpoise mortality in set nets.

Beginning in 1984, the National Marine Fisheries Service (NMFS) has conducted ship and aerial surveys of harbor porpoise abundance in California, Oregon, and Washington. This report presents results from four ship surveys. Results of the aerial surveys are presented by Barlow et al. (1988).

Porpoise density is estimated from survey data using line transect models (Burnham et al. 1980). Total abundance is estimated by extrapolating from density observed along transect lines to the entire area inhabited. Abundance in offshore regions is based on a model of porpoise density as a function of water depth. In addition to abundance estimation, survey data are used to examine the effect of environmental conditions on sighting efficiency and the possibility of temporal changes in harbor porpoise distribution.

METHODS

Ship Survey Methods

Surveys were conducted from two National Oceanic and Atmospheric Administration (NOAA) research vessels, the 52 m RV *David Starr Jordan* (Surveys 1, 3, and 4) and the 54 m RV *McArthur* (Survey 2)[5]. Both vessels were of similar design with viewing stations located on top of the pilothouse (viewing height was approximately 10 m above sea surface). Transect lines followed as close as possible to the 18 m isobath (roughly 2–4 km from the coast), although the actual depth along the transect varied from approximately 15–45 m, depending on the presence of local navigational hazards. The areas

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2]Diamond, S. L., and D. A. Hanan. 1986. An estimate of harbor porpoise mortality in California set net fisheries: April 1, 1983 through May 31, 1984. Adm. Rep. SWR-86-15, 40 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[3]Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California net fisheries April 1, 1984 through March 31, 1985. Adm. Rep. SWR-86-16, 38 p. Available from National Marine Fisheries Service, Southwest Region, 300 S. Ferry Street, Terminal Island, CA 90731.

[4]Dohl, T. P., R. C. Guess, M. L. Duman, R. C. Helm. 1983. Cetaceans of central and northern California, 1980–83: status, abundance, and distribution. Report prepared for U.S. Minerals Management Service, Contract #14-12-0001-29090, 284 p.

[5]Cruise reports available from the Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

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surveyed are shown in Figure 1. Survey design varied among the four trips:

Surveys 1 and 3 were in September 1984 and 1985, respectively. Both were designed to survey harbor porpoise density and abundance from Point Conception, CA to Cape Flattery, WA. An attempt was made to survey the entire coastline on each of these cruises, but several sections of the coast were missed (Fig. 1) because of fog and heavy weather. Five observation positions were used on these two surveys.

Survey 2 was from 24 January to 9 February 1985 and was primarily designed to examine seasonal changes in harbor porpoise distribution between Point Conception, CA and Cape Flattery, WA. Data from this cruise were not used for density or abundance estimation.

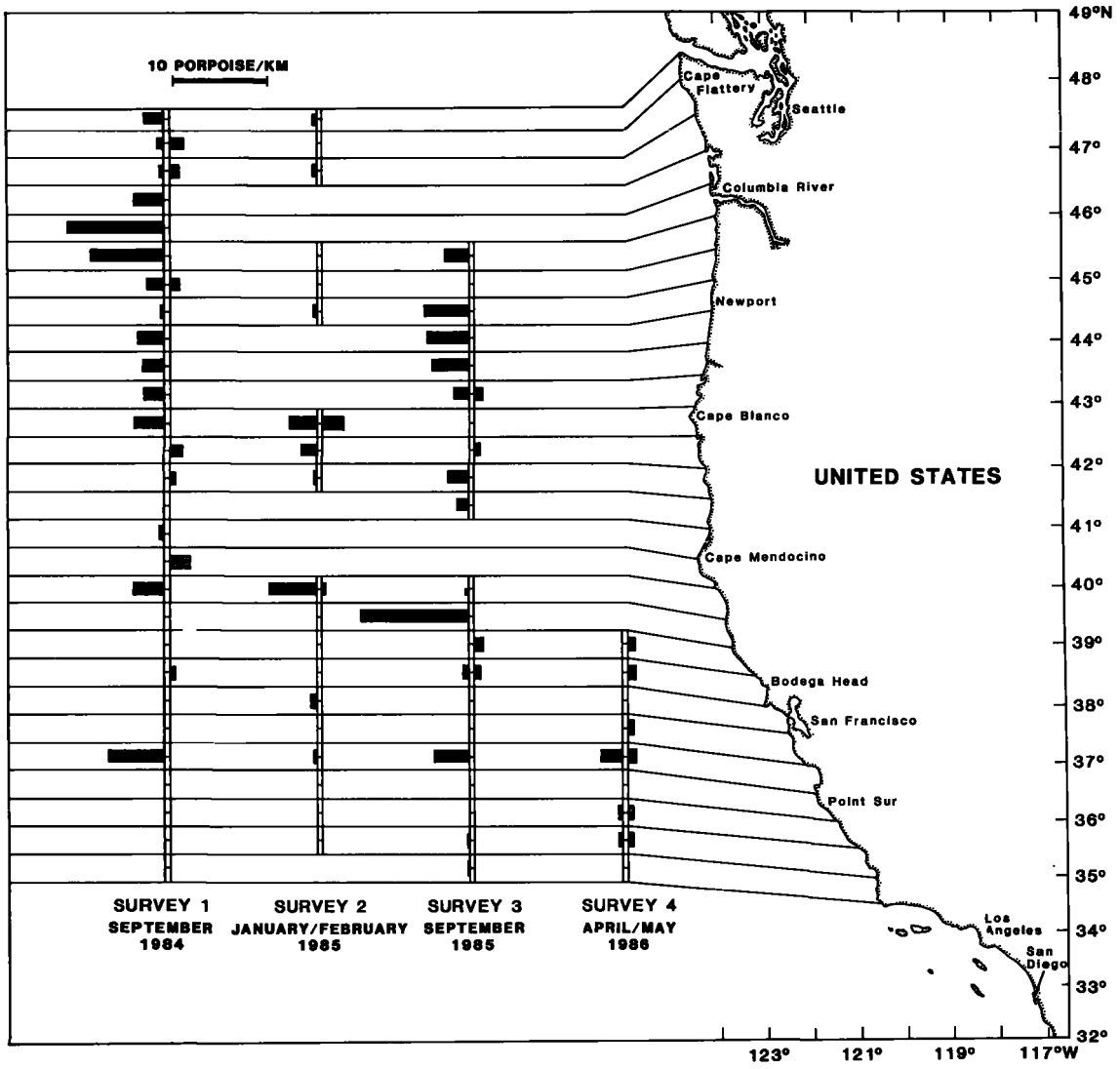

FIGURE 1.—Relative sightings per kilometer based on 30-minute latitudinal strata. Lines parallel to the coast indicate areas that were surveyed. Histograms indicate relative numbers of harbor porpoise seen per kilometer of transect, with bars to the left indicating relative numbers in calm seas (Beaufort 0, 1, and 2) and bars to the right indicating relative number in rough seas (Beaufort 3, 4, and 5).

Survey 4 was from 24 April to 5 May 1986 and was designed to investigate factors which affect harbor porpoise density estimation. The surveys concentrated on several areas of high porpoise density in central California. The vessel's activities were coordinated with a helicopter to gather information on the avoidance of the ship by harbor porpoise. Experiments were also conducted on survey 4 to determine whether an independent team of 3 observers would sight any porpoise that were missed by the primary team of 5 observers. Data from this survey were not used for density or abundance estimation.

Typically, 8–10 observers were used on each survey, with a rested observer starting every half hour and rotating through 5 primary observation positions at half-hour intervals. The 5 positions consisted of port and starboard inboard observers, port and starboard outboard observers, and a recorder positioned amidship. The inboard observers searched with 7 power (7×) binoculars from straight ahead to 90° (survey 1) or to 45° (surveys 2, 3, and 4) on their respective sides of the vessel. On survey 1 the outboard observers searched with 25×, pedestal-mounted binoculars. Although sightings could be made at great distances from the vessel using the 25× binoculars, these distant sightings contributed little to the estimation of trackline density, and use of 25× binoculars was discontinued. On subsequent surveys, both the inboard and outboard observers used 7× binoculars. The outboard observers searched from straight ahead to 90° on their respective sides of the vessel. The recorder searched in the immediate vicinity of the ship using unaided eyes and (intermittently) 7× binoculars.

On survey 2, only 3 observation positions were used from Point Conception to Point Sur, CA and from Point Reyes, CA to Cape Flattery, WA. When effort was reduced to 3 observers, the inside observation positions were eliminated.

On survey 4, a second team of 3 observers was added to monitor the effectiveness of the principal team. This monitor team searched using unaided eyes and (intermittently) 7× binoculars from the pilothouse deck (viewing height approximately 7 m from sea surface). The principal team and the monitor team did not communicate sighting information, and independent records were kept.

Data were noted by the recorder on data coding forms. Data on search effort included the beginning and ending times and positions for continuous legs of effort, the ship's heading and speed, personal identification codes for the observers, sea surface temperature, water depth, Beaufort sea state, sun position relative to the ship, and codes indicating the presence of rain or fog within 5 km. The ship position was determined from a Loran navigational system or by triangulation using coastal landmarks and dead reckoning. Ship speed was recorded directly from the Omega/Loran system or was calculated based on time and distance traveled between successive position fixes along straight transect lines. Water depth was measured using a 38 kHz acoustic depth sounder.

Data for sightings consisted of the above elements, plus estimated group size, distance to shore, an estimate of the angle between the trackline of the ship and the group, and an estimate of the distance from the ship to the group. Group size refers to all the individuals associated with a sighting event. In most cases, groups were closely associated individuals that surfaced together (mean = 2.92, median = 2.0). In two cases (Point Arena and Monterey Bay, CA), groups consisted of 50–80 loosely associated individuals that were organized in subgroups of 4–10). Group size was estimated and recorded independently by each observer; the mean of these estimates was used in subsequent analyses. The angle from the trackline to the porpoise was estimated visually with the aid of a pelorus mounted in front of the observer stations, or, when 25× binoculars were used, from a calibrated collar on the pedestal mount. On surveys 1 and 2, distances to harbor porpoise were estimated visually using the radar distance-to-shore as a reference, or, when 25× binoculars were used, distances were estimated using calibrated reticles in the oculars. On surveys 3 and 4, distances were estimated using calibrated reticles in the oculars of 7× binoculars. Data were also collected on the porpoises' direction of travel relative to the ship.

The length of a transect was estimated as the product of ship speed and elapsed time. To stratify density estimates by sea state, rain, and fog, the effort record was divided into segments during which the sea state, rain, and fog codes did not change.

In five areas, information was collected on variation in harbor porpoise density with water depth. During survey 3, three sections of the coast were surveyed intensively (Fort Bragg to Cape Vizcaino, CA; Cape Blanco to Coquille Point, OR; and Cape Lookout to Tillamook Head, OR), with transect lines following the 18, 56, 92, and 185 m isobaths. On survey 4, the 18 and 46 m isobaths were surveyed in Monterey Bay, CA and in the vicinity of the Russian River, CA. These data formed the basis of a model (below) to extrapolate porpoise density from

the usual transect lines (along the 18 m isobath) to deeper waters.

Helicopter Observations

During survey 4, a Hughes 500-D helicopter was used to collect information on harbor porpoise behavior in response to the survey ship. The helicopter flew approximately 10 km ahead of the vessel, and 3 observers in the helicopter looked for harbor porpoise. Once a group of harbor porpoise was sighted, the helicopter hovered at 200–300 m while observers made behavioral observations and periodically recorded the helicopter's position using an on-board Loran system. Fluorescein dye packages were dropped in the water to allow the helicopter to maintain its position when harbor porpoise were diving. Radio communication was maintained with personnel on the ship who also kept records of the helicopter position using radar distances and bearings based on returns from an X-band radar transponder in the helicopter. The ship changed course, when necessary, to ensure that it passed in close proximity to the porpoise that were being observed. Porpoise observers on the ship were not aware of the helicopter's activities and were not told of sightings made by the helicopter observers (although they were able to see dye patches in some cases). Behavioral observations from the helicopter included time spent at the surface, time spent diving, and direction of porpoise movement.

Density Estimation

Line transect methods were used to estimate the density of harbor porpoise from sightings. The assumptions of these methods are considered in detail in the discussion. The usual formula for estimating density (D) based on line transect surveys of small cetaceans is given by

$$D = \frac{f(0) \cdot n \cdot G}{2 \cdot L} \quad (1)$$

where $f(0)$ = the probability density function for sightings evaluated at zero perpendicular distance,
n = number of sightings of groups,
G = average group size calculated as the total number of individuals in all groups divided by the number of groups ($\Sigma N/n$), and
L = length of the transect.

(Holt and Powers 1982; Hammond and Laake 1983; Holt in press). I did not use mean group size explicitly in abundance estimation, and density of harbor porpoise individuals, D, was estimated as

$$D = f(0) \cdot (R/2) \quad (2)$$

where R = the number of individuals seen per length of transect ($\Sigma N/L$).

Equation (2) is functionally equivalent to Equation (1), but it simplifies variance estimation. Typically when using Equation (1), variances (and possibly covariances) must be estimated for $f(0)$, G, and n. Using Equation (2), variances are needed only for $f(0)$ and R, and covariance between mean group size and number of groups is handled implicitly. Sighting distributions appear to be independent of group size, G, (Results section), hence no adjustments were made to $f(0)$ for group size bias.

The parameter $f(0)$ is, in effect, a measure of sighting efficiency and should not vary with porpoise abundance. Sighting efficiency is, however, likely to change with sighting conditions, such as Beaufort sea state. Given these expectations and because relatively large sample sizes are needed to estimate $f(0)$ accurately, values for $f(0)$ were estimated for each survey by pooling all sightings within defined sea state categories. In order to estimate density on a finer scale, estimates of R were stratified by geographic region and multiplied by the pooled estimate of $f(0)$.

The sighting probability density function evaluated at zero distance, $f(0)$, was determined empirically by fitting curves to the frequency distribution of sightings as a function of perpendicular distance from the trackline (Burnham and Anderson 1976). Differences in distributions of perpendicular distance were tested using the Kolmogorov-Smirnov 2-sample test. To avoid bias due to rounding error, angle and radial distance data were "smeared" (Butterworth 1982; Hammond and Laake 1983). Angles were smeared by adding a uniformly distributed random number between $-5°$ and $+5°$ to angle estimates. Radial distances were smeared by adding a uniformly distributed random number between 0.2 and +0.2 times the estimated distance. These smearing levels were based on the degree of rounding that was apparent from the data (Barlow[6]).

[6]Barlow, J. 1987. Abundance estimation for harbor porpoise (*Phocoena phocoena*) based on ship surveys along the coasts of California, Oregon, and Washington. Adm. Rep. LJ-87-05.

Several models were investigated for estimating $f(0)$ from sighting distributions. The FORTRAN program Transect (Laake et al. 1979) was used to fit 2-, 3-, 4-, and 5-parameter Fourier series and 2-parameter exponential power series models. The FORTRAN programs Hazard and Hermite (S. Buckland[7]) were used to fit the 2-parameter hazard rate model (constrained such that parameter $P > 2$, Buckland 1985) and the 1-, 2-, 3-, and 4-parameter Hermite polynomial model (Buckland 1985). Of these models, the 2-parameter hazard rate model was selected based on its ability to fit the observed distributions and its lack of dependence on grouping criteria (Buckland 1985).

Perpendicular distances were grouped into strata, the size of which increased with perpendicular distance: 0–25 m, 25–50 m, 50–100 m, 100–200 m, 200–400 m, 400–800 m, 800–1,600 m, and 1,600–3,200 m. Several alternative groupings were investigated, and the choice of cutpoints made very little difference in estimates of $f(0)$. The above strata (increasing with distance) gave lower variances in $f(0)$ than when each stratum was of equal size (possibly because the hazard rate model assumes a distinct shoulder in the sighting distribution, and that shoulder is lost if the first distance strata are large).

No established criteria exist for choosing an appropriate perpendicular distance at which to truncate sighting distributions. Burnham et al. (1980) recommend that no more than 1–3% of sightings be eliminated by truncation. Using this recommendation, models were not able to adequately fit the observed sighting distributions. In this report, truncation distance was chosen in four ad hoc steps: 1) The hazard rate model was fit to perpendicular distance data truncated at distances of 400, 800, 1,600, and 3,200 m. 2) Truncation distances were identified which gave acceptable χ^2 values ($P > 0.1$). 3) Of the acceptable truncation distances, the standard error in $f(0)$ was estimated empirically by randomly drawing 10 samples (of the same size as the original sample) from the observed distribution of perpendicular distances and by calculating the standard deviation of $f(0)$ estimated from each random sample. 4) Truncation distances were chosen as those which gave the lowest coefficient of variation in $f(0)$.

Variance in R, the number of porpoise seen per kilometer, was estimated using jackknife statistics (Efron 1982). Jackknife estimates were calculated by first estimating the value of R using all data. The value, R_k, was again estimated excluding the kth segment of search effort. This process was repeated for each effort segment. To ensure that each kth segment was of equivalent length, effort segments with the same sea state, rain, and fog codes were combined in a linear array and were then divided into 10 segments of approximately equal length. The variance in the estimate of R was calculated as

$$s^2 = \frac{9}{10} \cdot \sum_{k=1}^{10} (R_k - \bar{R})^2 \qquad (3)$$

The variance of D was estimated using the Goodman (1960) product variance formula (assuming no covariance) using this jackknife variance for R and the above Monte Carlo variance for $f(0)$.

Fraction of Missed Animals

On survey 4, a second, independent team of 3 observers were used to estimate the fraction of harbor porpoise that are missed by the primary team of 5 observers. The fraction of missed animals in a sighting survey is analogous to the fraction of unmarked animals in a mark/recapture experiment (Pollock and Kendall 1987). This fraction was estimated using the Chapman (1951) modification of the Petersen (or Lincoln) index method (Pollock and Kendall 1987). Confidence limits were estimated using Adams' (1951) method, which assumes a binomial sampling distribution. Standard error was estimated using standard binomial formulas.

Abundance Estimation

A model was used to estimate the number of harbor porpoise along the entire coastline based on the density that was observed along the 18 m isobath. In shallow areas, such as the Bering Sea and Georges Bank, harbor porpoise are found a considerable distance from land (Gaskin 1984), hence offshore distribution is better modelled as a function of depth than as a function of distance from shore. (Although harbor porpoise are also found in very deep water in fjords and inland waterways of Alaska [Taylor and Dawson 1984], this represents a special case that is not applicable to coastal waters considered here.) The model used to estimate abundance was based on data collected on surveys 3 and 4 and on data from a ship surveys by La Barr and

Avail. from Southwest Fisheries Center, P.O. Box 271, La Jolla, CA 92038.

[7]S. Buckland, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1986.

Ainley[8] and Szczepaniak[9] in central California. The number of harbor porpoise seen per kilometer of transect was taken as an index of relative density along each isobath. A simple descriptive model was then constructed to give relative density as a function of water depth.

Fifteen depth strata were used in abundance estimation: 0–10, 10–20, 20–30, . . ., and 140–150 m. The surface area within the strata was calculated from digitized bathymetric data. Kelp beds were assumed to be unsuitable as harbor porpoise habitat; hence, kelp bed area was subtracted from the total area within the 0–10 m stratum. Kelp bed areas for the entire west coast were taken from Crandall (1915). More recent estimates for limited areas in central California are in good agreement with these previous values (G. Van Blaricom[10]).

For each of 15 depth strata, the abundance of harbor porpoise was estimated as the product of their density along the survey line (the 18 m isobath), the density in that depth strata relative to that along the survey line, the surface area included within that depth strata, and the inverse of the estimated fraction of trackline animals that were seen. Since survey effort and harbor porpoise density both varied geographically, abundance estimates were made for each of 8 geographic regions (Fig. 2). Areas within the depth strata were estimated from NOAA bathymetric data. The estimate of total abundance along the coast, N_T, is therefore given by

$$N_T = \frac{1}{F} \cdot \sum_{j=1}^{8} D_j \sum_{k=1}^{15} (I_k \cdot A_{j,k}) \qquad (4)$$

where D_j = density of individuals observed on the transect line in the jth geographic strata,

I_k = ratio of density in depth strata k to that on transect line (see Figure 4),

$A_{j,k}$ = area in geographic region j and depth strata k, and

F = the estimated fraction of trackline animals seen by the usual team of 5 observers.

Equation (4) was applied independently to the different surveys and, within surveys, to different sea state strata. When combining estimates from different sea states or different cruises, abundance was calculated as the mean of the densities in each of the stratum, weighted by the length of the transect line within that stratum.

In estimating standard error for total abundance, variances of products were calculated using the Goodman (1960) product variance formula, and variances of ratios were estimated using a Taylor approximation (Yates 1953, p. 198). Area was assumed to be known without error. Statistical error in the indices of abundance for the depth strata could not be estimated given the paucity of available information. To account for uncertainty in the model of depth distribution, three versions of the model are proposed to span a range of possibilities.

RESULTS

On the four surveys, 852 groups of harbor porpoise were sighted (an estimated 1,818 individuals). A distance of 6,590 km was surveyed during 56 days. The number of sightings per kilometer surveyed varied geographically and these geographic patterns appeared to change appreciably between cruises (Fig. 1).

Sighting Distributions

The number of sightings on the inshore and offshore sides of the vessels were approximately equivalent (383 and 392, respectively). The cumulative distributions of perpendicular sighting distances were not significantly different for these two sides ($P = 0.06$). Therefore, sighting distributions were assumed to be symmetrically distributed about the trackline, and the distributions of perpendicular sighting distances from both sides of the vessel were pooled for subsequent analyses.

The distributions of perpendicular sighting distances for the first three surveys were significantly different from one another ($P < 0.01$ for all). This was probably the result of the modifications in survey methods between these cruises. Surveys 3 and 4 used the same methods, and sighting distributions were not significantly different ($P = 0.39$). Given that changes in methods result in differences in sighting distributions, all surveys were treated separately in subsequent analyses.

Distributions of perpendicular distance were not significantly different between individuals sighted

[8]LaBarr, M. S., and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: A report of cruises in April and May–June 1985. Report to U.S. National Marine Fisheries Service, Northwest and Alaska Fishery Center, 7600 Sand Point Way N.E., Seattle, WA. Contract No. 41-USC252.

[9]Szczepaniak, I. D. 1987. Abundance and distribution of harbor porpoise (*Phocoena phocoena*) in the Gulf of the Farallones National Marine Sanctuary. Contract report prepared for National Park Service, Point Reyes National Seashore, Point Reyes, CA 94956.

[10]G. Van Blaricom, U.S. Fish and Wildlife Service, University of California, Santa Cruz, CA 93106, pers. commun. August 1986.

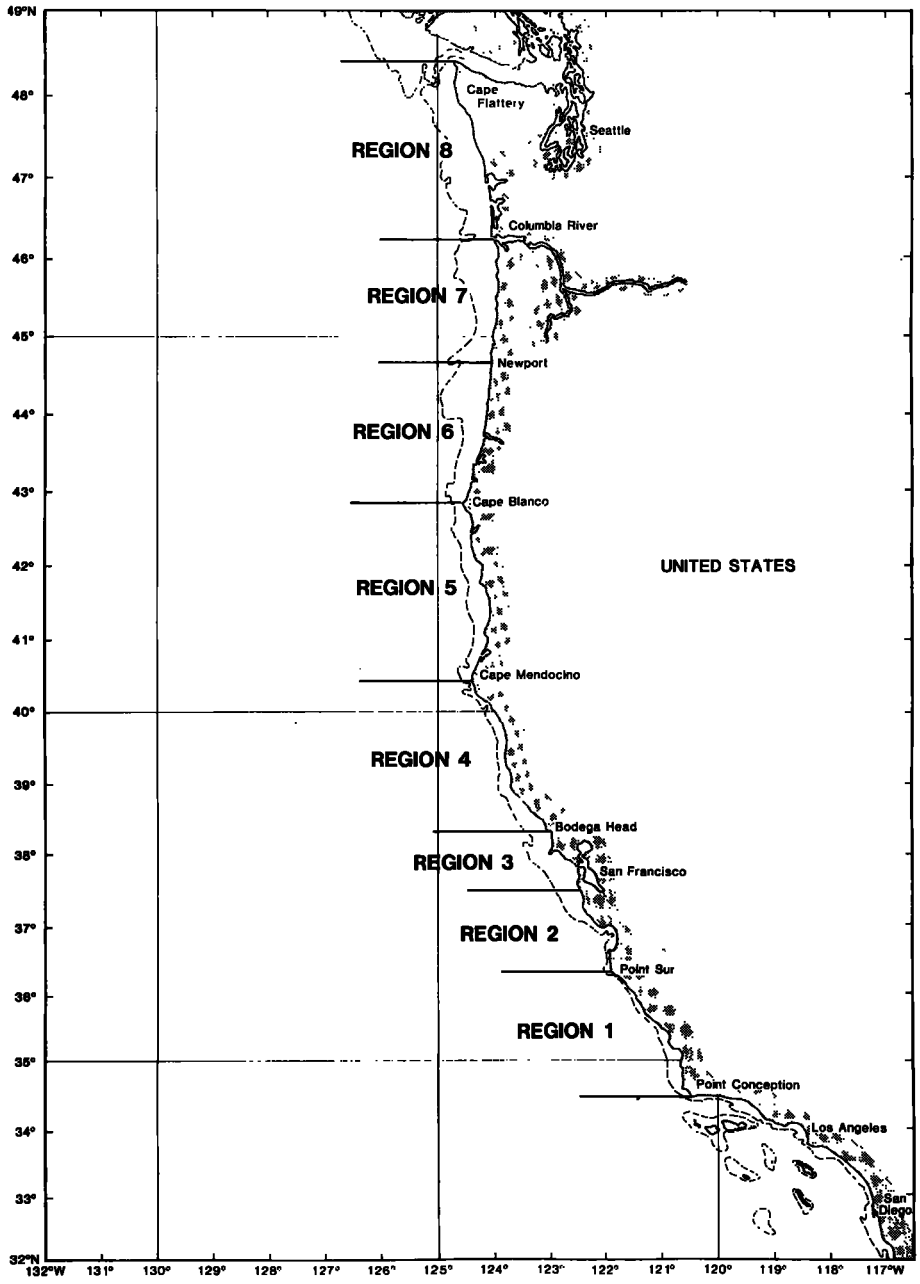

FIGURE 2.—Geographic regions used as strata in abundance estimation. Broken line indicates the 200 m isobath and delineates likely harbor porpoise habitat.

alone (group size of 1) and larger groups (group size of 3 and greater) (P = 0.56).

Environmental Conditions Affecting Sightings

Sighting efficiency was not significantly affected by rain, fog, or sun glare. Rain/fog conditions were considered "poor" if rain or fog were present within 5 km of the vessel and "good" if neither were present. The distributions of perpendicular sighting distances were not significantly different between these two strata (P = 0.32, 0.44, 0.78, and 0.64, respectively, for surveys 1, 2, 3, and 4), and the number of porpoise per kilometer surveyed was higher in the "poor" category for two of the surveys. Sun glare from the water's surface was considered to contribute to "poor" sighting conditions if the sun was within 45° of the trackline in front of the ship. Conditions were considered "good" when the sun was in other positions or was obscured by clouds. As with rain/fog conditions, the distributions of perpendicular sighting distances were not significantly different between these "good" and "poor" sun glare categories (P = 0.87, 0.47, 0.30, and 0.55, respectively, for surveys 1, 2, 3, and 4). The number of harbor porpoise per kilometer surveyed were slightly higher in the poor category for three of the surveys. In paired comparisons when glare was present on only one side of the bow, approximately equal numbers of sightings were made on the sides with and without glare (60 vs. 59, respectively). All categories of rain, fog, and glare are included in subsequent analyses.

Sea state did have a significant effect on porpoise sightings. Sea state was categorized as calm (without white-caps, Beaufort sea states 0, 1, and 2) or rough (with white-caps, Beaufort sea states 3, 4, and 5) following the classification used by Holt and Cologne (1987). Distributions of perpendicular distances were not significantly different between these categories for any of the surveys ($P > 0.05$); however for all surveys combined, the number of harbor porpoise detected per kilometer was much lower during rough seas (0.32 km^{-1}) than during calm seas (1.22 km^{-1}). There were insufficient sightings to estimate density for rough seas separately; therefore, rough sea data were excluded in subsequent analyses. For all three surveys, the numbers of harbor porpoise detected per kilometer was higher at Beaufort 0 & 1 than at Beaufort 2, and for survey 3, the distributions of perpendicular sighting distance were significantly different between these categories (P = 0.03). Porpoise density is, therefore, estimated separately for Beaufort 0 & 1 and for Beaufort 2 conditions. (For comparison, harbor porpoise abundance was also estimated pooling Beaufort sea states 0, 1, and 2. Estimated abundance was approximately the same by both methods, but the variance was slightly lower using the stratified sea state categories. For this reason, only the stratified estimates are presented here.)

Helicopter Observations

Helicopter observation of the behavior of harbor porpoise in response to the survey ship were made on only 6 groups of animals. Plots of vessel tracks and movements of the groups are given in the cruise report (see footnote 5). Only in one case was a distinct behavioral change noted in response to the ship. In that case, when the vessel was within 800 m, the group moved rapidly, perpendicular to the path of the vessel and then parallel to and in the opposite direction of the vessel. Observers on the ship saw this harbor porpoise group as they moved rapidly out of the path of the vessel. Observers on the ship also saw 2 of the other 5 groups. Although this sample of behavior is small, movement in response to the survey vessel appeared limited to within 1 km of the vessel and, when it occurred, animals did not travel far from their original positions.

Porpoise Density

The probability density distributions of perpendicular sighting distances are shown in Figure 3 for surveys 1 and 3 and for Beaufort sea states 0 & 1 and 2. The hazard rate model gave acceptable fits for all sighting distributions ($P > 0.1$) when the truncation criteria was set at 400 m (Table 1). For survey 1, the optimum truncation points were chosen as 400 m for Beaufort 0 & 1 and 800 m for Beaufort 2; for survey 3, this distance was 400 m for both Beaufort sea state categories. The fits of these models are shown in Figure 3. Estimates of density and standard errors are given in Table 2.

Depth Distribution Model

The model of harbor porpoise depth distribution was based on the relative densities of harbor porpoise at different water depths. Ship survey data were pooled into five depth ranges: 18–37 m (10–20 fathoms), 37–55 m (20–30 fathoms), 55–73 m (30–40 fathoms), 73–91 m (40–50 fathoms), and 91–110 m (50–60 fathoms). Ship surveys are generally not practical inshore of the 18 m isobath, but estimates

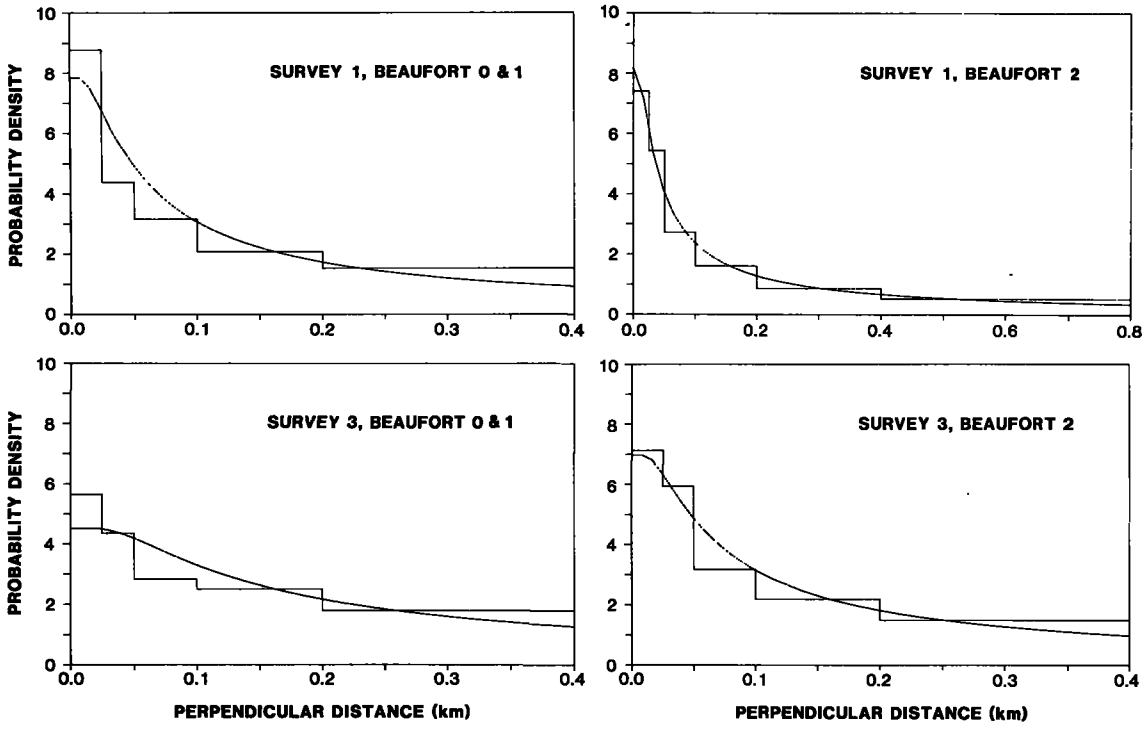

FIGURE 3.—Probability density distributions for perpendicular sighting distances. Histograms indicate observed distributions, and solid lines indicate the best fit of the hazard rate model to these data.

TABLE 1.—Estimated values of the probability density functions evaluated at zero perpendicular distance, $f(0)$. Estimates are based on the hazard rate model and were made for truncation distances of 400, 800, 1,600, and 3,200 m. Estimates are given only if the model gave an acceptable fit to the data ($P > 0.1$). Asterisks indicate $f(0)$ values with the lowest coefficient of variation (parentheses).

Survey	Beaufort sea state	Truncation distance 400 m	800 m	1,600 m	3,200 m
1	0 & 1	7.85 * (0.23)	5.31 (0.29)	4.31 (0.24)	— —
1	2	10.48 (0.59)	8.15 * (0.21)	7.09 (0.33)	5.78 (0.51)
3	0 & 1	4.51 * (0.22)	3.10 (0.66)	2.69 (0.31)	— —
3	2	6.97 * (0.19)	— —	— —	— —

from aerial surveys (Barlow et al. 1988) show roughly equal density at 0.61 and 1.85 km from the shore (the latter corresponding approximately to the 18 m isobath). Relative density from ship surveys was measured in the number of sightings per kilometer of searching effort. Relative densities at

TABLE 2.—Density estimates, D, for harbor porpoise (km^{-2}) along the 18 m isobath in each of eight geographic strata. Density was calculated per Equation (2), using estimates of $f(0)$ (Table 1) which had the lowest coefficients of variation. Values are not adjusted for missed animals. Standard errors are in parentheses.

Geographic region	Survey 1 Beaufort 0 & 1	Survey 1 Beaufort 2	Survey 3 Beaufort 0 & 1	Survey 3 Beaufort 2	Pooled estimates
1	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.1 (0.1)	0.04 (0.02)
2	1.1 (1.0)	0.0 (0.0)	0.6 (0.5)	0.1 (0.1)	0.51 (0.30)
3	—	0.0 (0.0)	0.1 (0.1)	0.0 (0.0)	0.03 (0.03)
4	—	2.5 (1.0)	0.0 (0.1)	6.7 (7.2)	2.83 (1.69)
5	—	2.1 (1.3)	0.8 (0.6)	0.6 (0.3)	0.91 (0.32)
6	1.4 (0.8)	2.0 (0.6)	2.5 (0.8)	2.6 (0.9)	2.22 (0.40)
7	7.9 (3.4)	0.8 (0.6)	2.5 (0.6)	1.3 (0.7)	2.64 (0.78)
8	1.8 (0.8)	0.0 (0.0)	—	—	1.09 (0.45)
Total	2.5 (1.1)	1.3 (0.6)	0.8 (0.4)	1.2 (0.5)	1.33 (0.30)

18–37 m show no consistent relationship to those at 37–55 m or 55–73 m (Table 3), but on average these appear to be approximately equal. Relative densities at 18–37 m are, however, consistently higher than densities at 73–110 m in all areas (Table 3). A total of 236 km were searched in waters deeper than 110 m and no harbor porpoise were seen.

Despite high variability in patterns of depth distribution and lack of ship coverage in shallow waters, some generalizations can be made about the depth distribution of harbor porpoise along the west coast. The relative abundance of harbor porpoise appears to be roughly constant from shore to 55 m, to be markedly lower at 73–110 m, and to be very low in waters deeper than 110 m.

Based on the above relationships, I propose the following preliminary model for the depth distribution of harbor porpoise along the coasts of California, Oregon, and Washington: constant abundance from the coast to the 80 m isobath, linearly decreasing abundance from the 80–120 m isobaths, and zero abundance in waters deeper than 120 m (Fig. 4a). Because considerable uncertainty exists in this model, I propose two alternative models (Fig. 4b, c). Alternative models b and c are less likely than the primary model given because both conflict with some of the available data. The alternative models do, however, encompass the likely range of relative density values and provide a means to evaluate the sensitivity of the abundance estimate to different models of depth distribution.

Fraction of Missed Animals

The experiment on survey 4 indicates that some trackline groups were seen by 1 group of observers and were missed by the other. A total of 103 sightings was made by both teams, 33 of which were estimated to be within 100 m perpendicular distance from the transect line. Of the 103 total sightings, 85 were detected only by the 5 principal observers, 6 were detected only by the 3 monitor observers, and 12 were detected by both teams. Of the 33 trackline sightings, 20 were detected only by the principal observers, 3 were detected only by the monitor observers, and 10 were detected by both teams. The Petersen estimate of the fraction of trackline porpoise seen by the primary team of 5 observers is thus 0.780 (SE = 0.117, 95% C.L. = 0.45–0.95). This indicates that approximately 22% of trackline sightings are missed by the principal teams of 5 observers.

Porpoise Abundance

Estimates of porpoise abundance in each of the eight geographic strata are given in Table 4 for the primary model of offshore distribution. Independent estimates are given for survey 1 and for survey 3

TABLE 3.—Relative harbor porpoise abundance observed within the specified depth ranges at a variety of study sites. Relative abundance is measured as number of porpoise sightings made per kilometer. Numbers in parentheses indicate kilometers surveyed.

	Depth range				
Location	18–37 m	37–55 m	55–73 m	73–91 m	91–110 m
Central California[1]	0.02 (89)	0.08 (172)	0.03 (403)	0.03 (279)	0.01 (166)
Gulf of the Farallones, CA[2]	0.29 (181)	0.00 (159)	0.30 (133)	0.00 (7)	0.00 (7)
Fort Bragg, CA	0.05 (41)	—	0.05 (43)	—	0.03 (35)
Coquille Pt, OR	0.24 (43)	—	0.35 (52)	—	0.08 (50)
Tillamook Head, OR	0.50 (57)	—	0.12 (52)	—	0.00 (17)
Monterey Bay, CA	0.46 (220)	0.29 (76)	—	—	—
Russian River, CA	0.00 (26)	0.30 (33)	—	—	—

[1]Data taken from LaBarr and Ainley (see text footnote 8) assuming an average survey speed of 9 knots.
[2]Data taken from Szczepaniak (see text footnote 9) assuming an average survey speed of 9 knots.

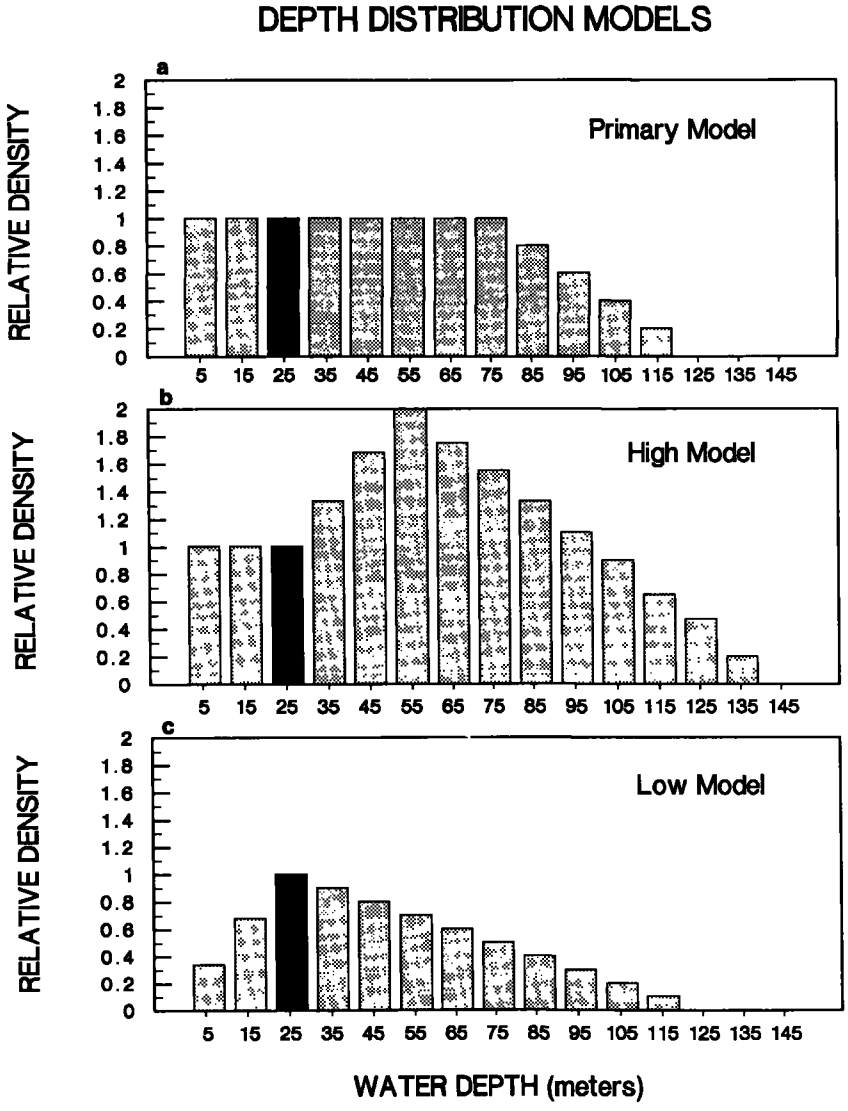

FIGURE 4.—Proposed models for the depth distribution of harbor porpoise expressed as relative densities, I_k, within 10 m depth intervals. Density at 20–30 m is assumed to be known and is given a relative value of 1. Figures represent a) a primary model of offshore distribution, b) a high estimate of offshore range, and c) a low estimate.

in each area. Both surveys show similar patterns, with higher abundances in the northern strata (4–8) and very low abundance in strata 1 and 3. Despite similar patterns, differences between the paired estimates are in some cases, large and statistically significant (t-tests, $P < 0.05$). Because region 8 was not covered on the third survey, it is not possible to compare estimates of total abundance for the entire coast between surveys. The total abundances for regions 1–7 (Point Conception to the Columbia River) are 46,550 (SE = 10,932) animals and 32,029 (SE = 10,906) animals for surveys 1 and 3, respectively. The difference between these estimates is not statistically significant (t-test, $P > 0.05$). Pooling the results of the two surveys, the estimate of harbor porpoise abundance between Point Conception and Cape Flattery in September of 1984 and 1985 is 45,713 (SE = 7,865) animals (Table 4). The same estimate using the alternate models of offshore distribution ranges from 28,769 to 78,019 (Table 5).

TABLE 4.—Estimated abundance of harbor porpoise in each of the eight geographic strata based on the primary model of offshore distribution. Estimates for Beaufort 0 & 1 and for Beaufort 2 were computed separately and then averaged, weighting by transect length. Pooled estimates for the eight strata were obtained as an average of the two surveys, weighting by transect length. All estimates are adjusted for missed animals. Standard errors are in parentheses.

Geographic region	Survey 1	Survey 3	Pooled estimates
1	0	126 (68)	96 (52)
2	2,401 (2,180)	932 (646)	1,459 (885)
3	0	153 (158)	112 (116)
4	6,909 (2,959)	9,096 (9,855)	7,909 (4,784)
5	11,245 (6,943)	3,296 (1,410)	4,806 (1,745)
6	9,061 (2,724)	12,786 (3,676)	11,107 (2,363)
7	16,934 (7,097)	5,641 (2,424)	10,416 (3,311)
8	9,808 (4,311)	—	9,808 (4,311)
Totals			
Regions 1–3	2,401 (2,180)	1,210 (669)	1,667 (895)
Regions 1–7	46,550 (10,932)	32,029 (10,906)	35,904 (6,578)
Regions 1–8	56,358 (11,751)	—	45,713 (7,865)

TABLE 5.—Estimated abundance of harbor porpoise in central California (regions 1–3) and along the entire coast (regions 1–8) based on two alternate models of offshore distribution. All estimates are adjusted for missed animals. Standard errors are in parentheses.

	Survey 1	Survey 3	Pooled estimates
Alternate Model b			
Regions 1–3	3,966 (3,602)	1,986 (1,104)	2,744 (1,478)
Regions 1–8	95,132 (19,515)	—	78,019 (13,356)
Alternate Model c			
Regions 1–3	1,505 (1,367)	770 (421)	1,054 (561)
Regions 1–8	35,736 (7,550)	—	28,769 (4,995)

DISCUSSION

Distribution

Harbor porpoise are not uniformly distributed between Cape Flattery and Point Conception. Although there are no obvious discontinuities within this range, density varies geographically and temporally. The most dramatic temporal changes are between the two September surveys and the January–February survey (Fig. 1). The coasts of Washington and northern Oregon were found to have relatively high densities of harbor porpoise in September, but, despite excellent sighting conditions, very few porpoise were seen there in January. High densities of harbor porpoise were also seen in Monterey Bay on both September cruises and on survey 4 in May. This area was intensively surveyed in February, and few harbor porpoise were seen. As can be seen in Figure 1, adjacent areas tended to have similar densities within a survey. Less consistency is found when the same areas are compared between different surveys.

The apparent changes in distribution could be caused by small changes in depth distributions. The majority of survey effort was along the 18 m isobath. A large fraction of animals could be missed if their depth distribution changed by 10 m or less. More information on depth distributions is needed before the apparent temporal changes in geographic distribution can be interpreted.

Porpoise Density

Estimates of harbor porpoise density ranged from 0.03 to 2.8 animals/km^2 along transect lines in the eight geographic regions (pooled estimates, Table 2). In another study, Szczepaniak (fn. 9) estimated 0–1.9 porpoise/km^2 in four study areas in the Gulf of the Farallones, CA. Taylor and Dawson (1984) found 1.2–5.9 porpoise/km^2 at study sites in Glacier Bay, AK. Flaherty and Stark[11] estimated 0.8–1.6 porpoise/km^2 in Washington Sound. Densities in the present study are therefore within the range of densities found in other areas along the same coast.

Harbor porpoise density was estimated for California, Oregon, and Washington based on aerial surveys that were concurrent with the present study (Barlow et al. 1988). The overall estimate of harbor porpoise density from that study (corrected for missed animals) was 1.79 porpoise/km^2. The overall estimate from the ship survey (1.33 porpoise/km^2) can be corrected for missed animals to yield an estimate of 1.73 porpoise/km^2. Given that the coef-

[11]Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound". Final Report #80-ABA-3584 submitted to National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, 7600 Sand Point Way, NE, Seattle, WA 98115. 84 p.

ficient of variation in the pooled ship estimates is nearly 25%, these estimates are in very close agreement. However, because the aerial estimates are based only on the small fraction of the coastline that was surveyed under optimal conditions, the ship estimates are probably a better representation of porpoise density for the entire coast.

Of the areas surveyed, harbor porpoise density is highest in northern California and Oregon. The highest density was seen in northern Oregon (region 7) during survey 1. The second highest density was observed in northern California between Bodega Head and Cape Mendocino (region 4) on survey 3.

Two areas in central California (regions 1 and 3) were found to have very low densities. Region 1 includes the Big Sur coastline from Point Conception to Point Sur. This area is characterized by steep depth gradients and hence has little habitat that is suitable for harbor porpoise. Region 1 was relatively well covered, with 378 km of trackline surveyed at Beaufort sea states 0–2. In contrast, region 3 includes the Gulf of the Farallons with its broad coastal shelf within the 100 m isobath. Based on surveys of 764 km, Szczepaniak (fn. 9) estimated 1,033 harbor porpoise are found in the Gulf of the Farallones alone. This is much greater than my estimate of 112 animals in region 3 based on only 175 km of survey effort. Because of his greater amount of search effort in this area, I believe that Szczepaniak's estimates for region 3 are more accurate than mine. Although regions 1 and 3 were both identified as low density areas, more confidence can be placed on this conclusion for region 1 than for region 3.

Abundance

The size and behavioral characteristics of harbor porpoise make estimating their abundance difficult. Harbor porpoise are small, occur in groups of only a few individuals, and surface without conspicuous splashes; their distribution is extremely patchy. Even with 5 observers, the effective path width that can be searched from a ship is <1 km, and that path width decreases very rapidly in rougher sea states. All of these factors contribute to high variability in the abundance estimates presented here. Seasonal and year-to-year changes in the distribution of harbor porpoise may also contribute to the variability seen within geographic strata. These are, however, the best (and, for some regions, the only) estimates of harbor porpoise abundance for the study area.

Although there are no prior estimates for Oregon or Washington coasts, Dohl et al. (fn. 4) estimated harbor porpoise abundance in central and northern California. Their estimates range from 3,000 harbor porpoise in autumn to 1,600 in summer, which correspond (approximately) to the pooled estimate of 11,457 for regions 1–4 based on the present study. There are, however, several problems with the application of their methods to the estimation of harbor porpoise abundance. In a direct comparison with shore counts, Kraus et al. (1983) showed that observers on aircraft saw only 10–20% of harbor porpoise groups. Dohl et al. (fn. 4) did not apply a correction to account for harbor porpoise groups that are submerged at the time the aircraft passed. Also, Dohl et al. did not stratify estimates by distance from shore or depth. Although most of their harbor porpoise sightings were within 0.5 km (0.25 nmi) of shore, their density estimates were extrapolated to an area extending 166 km from the coast. Estimates from the current study are based on better methodology than previous estimates.

In addition to exposed coastal habitats, harbor porpoise are also found in bays along the coasts of California, Oregon, and Washington. Goetz (1983) reported that harbor porpoise are found throughout the year in Humboldt Bay, CA. Harbor porpoise have been seen in San Francisco Bay, but are described as rarely present[12]. Abundance of harbor porpoise in inland waters may, however, vary seasonally (Taylor and Dawson 1984). No estimates exist for the total number of harbor porpoise inhabiting bays. Survey effort in the present study was limited to exposed coastal areas (including Monterey Bay, but excluding San Francisco Bay, Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor). If harbor porpoise density in bays were the same as that which was observed along the 18 m isobath, population sizes presented here could be increased by approximately 3.1% to account for porpoise inhabiting 900 km^{-2} (the approximate combined area of Humboldt Bay, Coos Bay, Yaquina Bay, the mouth of the Columbia River, Willapa Bay, and Grays Harbor).

Line Transect Assumptions

Biases in abundance estimates can be an even greater problem than high variability. In the case of estimates presented here, biases could be introduced if the assumptions of line transect sampling

[12]Szczepaniak, I. D., and M. A. Webber. 1985. Status of the harbor porpoise (*Phocoena phocoena*) in the eastern North Pacific, with an emphasis on California. Contract report to the Center for Environmental Education, Washington, D.C., 52 p.

are not met (Burnham et al. 1980; Hammond and Laake 1983). Of these assumptions, the most relevant to this study are 1) the area must be sampled randomly or the animals must be randomly distributed within the area; 2) all groups on the trackline must be detected; and 3) group size must be estimated without error. These assumptions will be addressed below.

To address the first assumption (random distribution), cruise tracks were chosen to systematically cover the coast from Point Conception to Cape Flattery. Because the surveys were designed to cover the entire longshore range of harbor porpoise in this area, randomly placed survey tracks were deemed unnecessary. Although some areas of the coast were missed, these locations were determined by weather and were presumably not correlated with porpoise abundance. Surveys were, however, limited to a very narrow strip along the 18 m isobath. Initially, the choice of this survey track was based on the observation that, in aerial surveys, harbor porpoise were usually found within 0.5 km (0.25 nmi) of the shoreline in California (Dohl et al. fn. 4). The 18 m isobath was simply the shallowest reasonable working depth for the NOAA survey ships. In the course of these surveys, it was found that harbor porpoise are commonly distributed much further from the coast than 0.5 km and that one survey track could not adequately cover their habitat. The offshore distribution of harbor porpoise is not random, but is related to water depth, distance from shore, or both. The model from which I extrapolated density at 18 m to density at other depths was based on a rather limited sample at a few locations along the coast. The assumption of random search in offshore areas was not met. Additional work is required to evaluate the effect of this.

The second assumption is that 100% of the animals in the immediate vicinity of the trackline were detected. Animals near the trackline can be missed because they move away from the path of the ship, because they do not surface within the visual range of the observers, or because the observers fail to detect animals that do surface. Any of these would result in a negative bias and an underestimation of porpoise abundance using line transect methods. These three problems are considered in more detail.

West-coast harbor porpoise are commonly said to avoid vessels (Flaherty and Stark fn. 11; Szczepaniak and Webber fn. 12) and may be missed or not counted in the proper perpendicular distance category for this reason. On the surveys, the majority of harbor porpoise were oriented roughly parallel to the ship at the time they were sighted and were swimming parallel to the ship and in the opposite direction (see footnote 5). This was also observed in one instance from the helicopter; however, in that case the group first moved perpendicular to the path of the ship. These observations indicate that harbor porpoise are reacting to the ship before they are seen by observers. Reaction to and avoidance of the ship does not necessarily mean that estimates of trackline density are biased if animals are detected before they travel an appreciable distance from the trackline. In several instances, harbor porpoise surfaced within 50 m of the ship and directly in its path. These animals appeared startled and quickly moved to avoid the ship. In these cases, the rapid movement of the animals and splashes associated with that movement made the animals more visible to observers. Because avoidance behavior may make harbor porpoise more visible and because the distributions of perpendicular distance show only a single mode (at the origin), vessel avoidance probably does not introduce a large bias in harbor porpoise abundance estimation. More work is needed in this area.

Harbor porpoise near the trackline may also be missed if they either inadvertently or intentionally do not surface within the visual range of the observers. Typical mean dive times for harbor porpoise have been measured as 1.5–2.3 minutes (Glacier Bay, AK; Taylor and Dawson 1984), 1.8 minutes (northern Oregon; B. Taylor[13]), and 0.4–1.4 minutes (Bay of Fundy; Watson and Gaskin 1983). The ships' speed during surveys was approximately 18.5 km/h or 310 m/min; thus, in 2 minutes the ship would travel 620 m. The average distance at which animals were first seen was 704 m from the ship. If individual dive times were appreciably longer than 2 minutes, some trackline individuals would not be detected by observers. In data collected in northern Oregon, 16% of dive times were greater than 2.5 minutes (B. Taylor fn. 13). In addition, harbor porpoise have been reported to increase dive times up to 7 minutes in the presence of boat traffic (Flaherty and Stark fn. 9). (This latter estimate is considerably longer than any other published estimate, and it is possible that those researchers missed one or more surfacings). Helicopter observations in Monterey Bay indicated that porpoise groups did not extend dive times in the presence of the survey vessel (see footnote 5). This area might not be representative, however, because harbor porpoise may

[13]B. Taylor, Department of Biology, University of California, San Diego, CA 92093, pers. commun. August 1986.

be more accustomed to vessel traffic there than along the majority of the coast. It is likely that some harbor porpoise are missed because they do not surface near the vessel; however, it is not possible to quantify this source of bias without additional study.

Trackline animals may be missed even if they do not avoid the ship and do surface within visual range of the observers if their surfacing is not detected. In another study comparing ship surveys to aerial and shore surveys, Kraus et al. (1983) found that observers on ships saw only about 50% of the harbor porpoise in an area. In that study, however, ship observers stood only 2.5 m above the sea surface (versus 10 m in this study), and the estimate of 50% was based on all groups, not just on trackline animals. Based on the experiment using monitor observers in the present study, an estimated 22% of harbor porpoise that surface on the trackline are missed by the usual team of 5 observers. If this is underestimated by some percentage, population size would be underestimated by the same percentage.

The third critical assumption is that group size is estimated without error. In the case of harbor porpoise, group size is small and estimates are typically based on actual counts. For tropical dolphins, which school in groups of several hundreds, the problem of group size estimation is more acute (Holt and Powers 1982; Hammond and Laake 1983). Only in two instances did harbor porpoise group size exceed 20: in Monterey Bay and near Point Arena, both in California. Excluding these two sightings, mean group sizes are 2.05, 2.33, 2.03, and 1.59 for surveys 1, 2, 3, and 4 (respectively); including the two sightings, means are 2.30 and 2.26 for surveys 1 and 3. These values are comparable to other estimates of mean group size for coastal populations of harbor porpoise: 2.2 based on aerial surveys in California (Dohl et al. fn. 4), 2.6 based on ship surveys in the Gulf of the Farallons (Szczepaniak and Webber fn. 12), 2.3 based on shore surveys in northern Oregon (see footnote 5), and 2.75–3.23 based on aerial surveys along California, Oregon, and Washington (Barlow et al. 1988). The consistency of all these estimates from different platforms indicates that group size estimation from ships is not likely to be a major source of bias in abundance estimation.

Variance Estimation

Although the estimates of standard error for abundance and density are very high, these may still be underestimates because the choice of a truncation criterion was based on minimizing variance and because all possible sources of sampling errors were not considered. The model upon which relative abundance in the various depth strata was based is too crude to allow reasonable estimates of its variability. Estimates based on alternate models of depth distribution indicate that abundance estimation is relatively sensitive to the choice of models. Additional field work may help refine this model and allow estimation of variance for the parameters I_k in Equation (4).

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HARBOR PORPOISE, *PHOCOENA PHOCOENA*, ABUNDANCE ESTIMATION FOR CALIFORNIA, OREGON, AND WASHINGTON: II. AERIAL SURVEYS

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ABSTRACT

We conducted aerial surveys in September 1984 and September and October 1985 to determine the abundance of harbor porpoise along the coasts of California, Oregon, and Washington. Two observers and a recorder searched along predetermined transect lines at 0.61 and 1.85 km offshore. Strip transect methods were used. A total of 366 groups of harbor porpoise were seen in the 9,500 linear kilometers that were surveyed. Apparent density was significantly affected by sea state and cloud cover. Using observations made during optimal conditions (clear skies and calm seas), apparent harbor porpoise density averaged 0.56 animals km^{-2}. Behavioral observations from shore and from a helicopter indicated that porpoise are near the surface only 23.9% of the time. To account for this, porpoise density was multiplied by a factor of 3.2, resulting in an adjusted estimate of 1.79 animals km^{-2}. Only a small percentage of the total area inhabited was surveyed under optimal sighting conditions, hence density estimates were not extrapolated to estimate total porpoise abundance. Harbor porpoise density showed similar patterns to those measured from ship surveys, and adjusted aerial estimates are approximately equal to ship estimates.

Harbor porpoise, *Phocoena phocoena*, are subject to mortality in the halibut set net fishery in central California (NMFS[4]; Diamond and Hanan[5]). To evaluate the significance of this mortality, an estimate of population size is needed. Two aerial surveys and three ship surveys were conducted from 1984 to 1986 to gather information on harbor porpoise abundance along the coasts of California, Oregon, and Washington. Observations were also made from shore-based stations and from a helicopter to provide ancillary information needed for population estimation. Results and population estimates from the ship surveys are reported by Barlow (1988). Preliminary results from the 1984 and 1985 aerial surveys were presented by Oliver and Jackson[6] and Oliver[7], respectively. Here we present population density estimates based on the aerial surveys and on shore and helicopter observations.

The aerial surveys were flown in September of 1984 and in September and October of 1985 from Point Conception, CA to Cape Flattery, WA. Surveys were coordinated by the National Marine Fisheries Service (NMFS) in collaboration with the California Department of Fish and Game, the Oregon Department of Fish and Wildlife, and the Washington Department of Wildlife. Survey design was based on information given by Dohl et al.[8] regarding harbor porpoise distribution in California. They reported that harbor porpoise were usually

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found within 0.25 nautical miles (nmi) of the shoreline. We therefore designed our aerial surveys to cover a very narrow coastal band. Subsequent information from ship surveys (Barlow 1988) has shown their distribution to extend considerably farther from the coast. Therefore, estimates of porpoise density from aerial surveys apply to a relatively small portion of harbor porpoise habitat. For this reason we do not estimate population size by extrapolating aerial density estimates to the entire area inhabited. The density estimates presented here are used to corroborate estimates based on ship surveys and to estimate density for areas that were too shallow to be surveyed by ship.

Based on previous studies of dive times (Watson and Gaskin 1983; Taylor and Dawson 1984) we expected a proportion of the harbor porpoise to be diving and therefore missed by aerial observers. Shore-based studies were conducted in September 1985 from cliffs in northern Oregon to determine average dive times for west-coast harbor porpoise. Helicopter observations were made in April and May 1986 in Monterey Bay and near Bodega Head, CA to gather dive time information and obtain a direct measure of the fraction of time that harbor porpoise groups are visible from the air. These two samples did not differ significantly from previous samples of harbor porpoise in Alaska, so all samples were pooled to adjust estimates of porpoise density from aerial surveys to account for the probability of missing submerged animals.

METHODS

Aerial Survey Methods

Strip transect methodology (Seber 1973) was used during the aerial surveys. This method assumes that all individuals within a transect strip are detected. Transect lines were flown parallel to the coast line at distances of 0.61 and 1.85 km (0.33 and 1.0 nmi) offshore. Transect strips of equal width were surveyed on both sides of the aircraft. The margins of the strips were denoted by tape marks or streamers on the wing struts. Strips were divided into inside and outside swaths of unequal width (Fig. 1) by a third tape mark or streamer between the other two. When porpoise were sighted within the transect strip, the pilot was directed to leave the transect line and circle over the porpoise to obtain an accurate count of the number within the original group that was sighted. If additional groups or individuals were sighted during this circling, they were excluded from density estimates. Porpoise density, x, was calculated as the number of individuals sighted within a transect, n, divided by the product of the transect width, w, times the distance, d, that was flown:

$$x = n/(W \cdot d) \quad (1)$$

We used both single and twin-propeller, high-wing, 4-passenger aircraft in our surveys. The search team consisted of two observers seated in the right and left passenger seats. A data recorder sat in the copilot's seat and did not search. If the recorder sighted animals that were missed by the observers, these were noted but were not included in density estimates. The planes were flown at an altitude of 213 m (700 feet) and at an airspeed of 158–167 km/h (85–90 knots). The original survey plan called for all sections of the coast to be covered twice on each survey. This was accomplished in 1984, but poor weather in 1985 resulted in the Washington coast and part of the Oregon coast being covered only once. The dates flown and areas covered are given in Table 1.

TABLE 1.—Dates, areas covered, and observer teams during aerial surveys for harbor porpoise. Geographic regions refer to those shown in Figure 2. Observer team refers to a pair of individuals.

Date	Regions covered	Observer team	Distance to shore (km)
9/09/84	7,8	A	0.61
9/10/84	5,7	A	0.61
9/11/84	5,6	A	0.61
9/13/84	1,2,3,4,5	B	0.61
9/14/84	1,2,3,4,5	B	0.61
9/17/84	1,2,3,4	B	0.61
9/18/84	1,2,3,4	B	0.61
9/11/85	6,7	C	0.61
9/16/85	1,2,3	D	0.61
9/17/85	4	D	0.61
9/18/85	4,5	D	0.61,1.85
9/19/85	4,5	D	0.61,1.85
9/20/85	2,3	D	1.85
10/04/85	7,8	E	0.61
10/14/85	1,2,3	D	1.85
10/15/85	4,5	D	1.85

Data gathered on both the 1984 and 1985 surveys were similar in format. Recorded data on sighting conditions included Beaufort sea state, a measure of cloud cover, a code indicating the presence of haze or fog, sun position relative to the aircraft, and a subjective measure of the observers' ability to see into the water through turbidity, surface reflection and diffraction. The latter was called surface penetration and was recorded separately for each of the

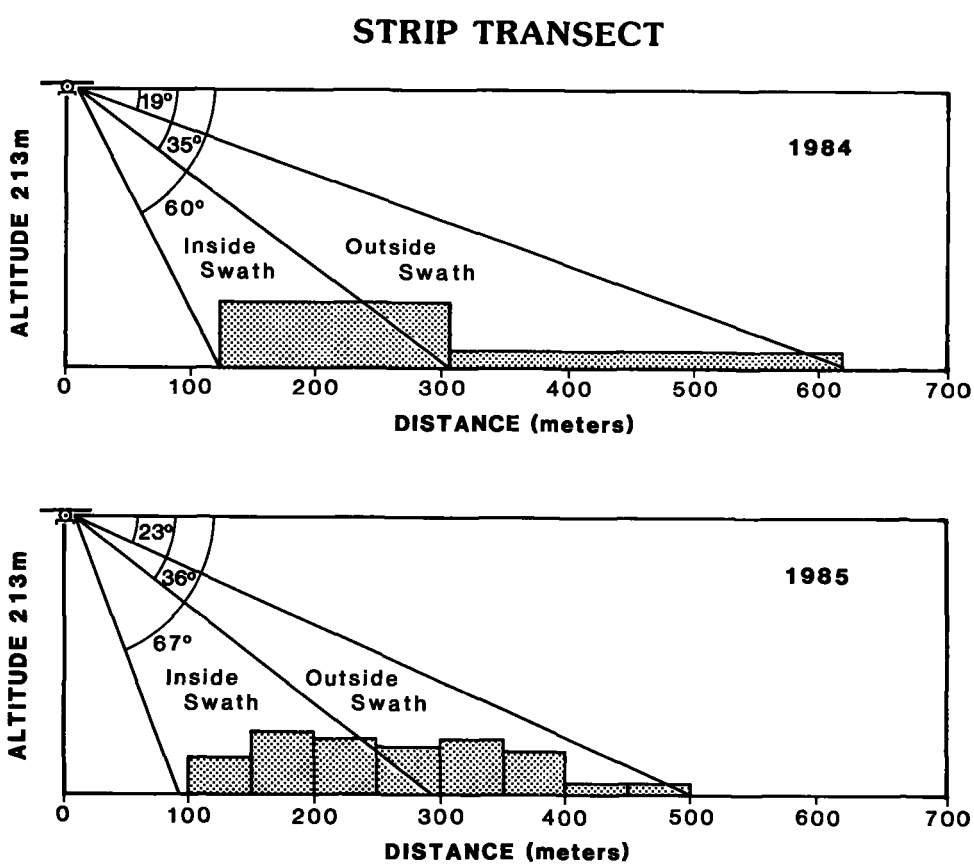

FIGURE 1.—Configuration of transect strip widths and distributions of perpendicular sighting distances for aerial surveys in 1984 and 1985. Angles are given as declinations from horizontal. Histograms indicate the relative number of porpoise seen in the given distance interval.

four swaths (inside and outside on both sides of the aircraft). In severe sun glare conditions, searching was discontinued for one or both swaths on one side of the aircraft. Additional data included individual observer numbers, date, time, and position (measured to 10ths of minutes of latitude and longitude). All of these data were recorded at the beginning and end of continuous transects and whenever conditions changed or a sighting was made. Additional data were recorded for marine mammal sightings, including a code for the species of animal seen, an estimate of the number of individuals, a code indicating on which side of the aircraft the animals were seen, and a code indicating in which of the swaths the animals were found (inside, outside, or, if the animals were not within the designated strips, neither).

An attempt was made to gather the above information in a similar manner for both surveys. Some differences in subjective measures of sighting conditions could, however, be expected because there was no overlap in observers between years. In addition, there were some differences in design between the 1984 and 1985 surveys. In 1984, the inside and outside swaths were from 123 to 305 m and from 305 to 620 m, respectively (as measured from the midline of the transect). The margins of these swaths corresponded to declinations angles of 19°, 35°, and 60° (Fig. 1). In 1985, the swaths were 91–294 m and 294–503 m and corresponded to declination angles of 23°, 36°, and 67° (Fig. 1). In 1984, effort was concentrated on the inside swath and the outside swath was not intended for abundance estimation. The change in swath size was intended to reduce the total area being searched, thus potentially allowing the outer swath to be used for density estimation. In 1985, effort was divided equally between the two swaths. During the 1985

surveys the declination angle to marine mammals was measured when the animals were perpendicular to the aircraft using hand-held inclinometers. Declination angles were not measured during the 1984 survey.

Distance to the coast was monitored using declination angles (19° for 0.61 km and 6° for 1.85 km). On the 1984 survey, this distance was 0.61 km for the entire survey. During the 1985 survey, we surveyed at both 0.61 and 1.85 km from the coast. In 1984, the coast was taken to be the outer limit of the surf zone. In 1985, the coast was taken to be the outer limit of the surf zone or, if kelp beds were present, the outer margin of those beds.

Shore Observation Methods

Observations of harbor porpoise diving behavior were made from rocky headlands in northern Oregon (Tillamook Head, Neahkahnie Mountain, Cape Meares, and Cape Lookout) immediately before the second aerial survey (7–11 September 1985). Observers were equipped with 7×50 binoculars with compasses and ocular reticles and a single 20×120 binocular. Ventilation data were collected whenever possible and included the number of animals at the surface and the length of time spent at the surface. Observations were recited aloud by the observer and were written down by a second person or were recorded onto magnetic tape. The ventilation cycle typically consisted of a period with several surfacing rolls and breaths (which we call a surfacing series) followed by a much longer period of submergence (which we call a dive). This dive cycle corresponds to ventilation pattern B as described by Watson and Gaskin (1983) for harbor porpoise in the Bay of Fundy and the pattern described by Taylor and Dawson (1984) for porpoise in Glacier Bay.

Helicopter Observation Methods

Behavioral observations were also made by three observers in a 4-passenger, jet-turbine helicopter. Upon locating a group of harbor porpoise, a fluorescein dye marker was dropped and the helicopter hovered or circled slowly above the group at an altitude of approximately 300 m. The number of animals, the time they were visible at the surface, and the dive times were recorded, along with information on cloud cover, sea state, and water turbidity. Each behavioral session was given a subjective rating based on how well the observers could follow the group and obtain accurate dive times. Only sessions with good or excellent ratings were included in analyses.

Probability of Missing Submerged Animals

Given that a porpoise would be within the visual range of an observer, the probability that it will be at the surface during the passage of the aircraft is related to the average time it spends at the surface, s, the average time spent below the surface, d, and the window of time during which it is within the visual range of an observer, t. This probability was calculated as

$$Pr(\text{being visible}) = \frac{s + t}{s + d}. \quad (2)$$

The probability of missing a submerged animal is equal to the complement of this value.

Density Estimation

Density of harbor porpoise was estimated as the number of animals seen divided by the area searched (Equation (1)). This raw density estimate was adjusted by dividing by the probability that an animal would be visible from the air at any given instant (Equation (2)). The area searched was estimated as the swath widths times the lengths of the transects. Transect lengths were calculated as the sum of the great circle distances between successive position fixes. Densities were calculated for each of the eight statistical regions used by Barlow (1988) (Fig. 2).

The statistical difference in harbor porpoise density between different sighting conditions or different areas was tested using the raw density estimates. Density estimates for short transects were frequently zero, thus violating the parametric assumptions of normally distributed, homoscedastic error. Nonparametric tests were therefore chosen for density comparisons. In discussing statistical tests, a transect segment refers to the length of transect line between two successive position fixes and are typically <20 km. The measured variables relating to sighting conditions are constant within a segment, and because each sighting is accompanied by a new position fix, a segment will contain at most, one sighting.

Whenever applicable, the Wilcoxon paired-sample test (Wilcoxon 1945) was used to test one factor while controlling for as many other factors as possible. Ten paired measures of density were created

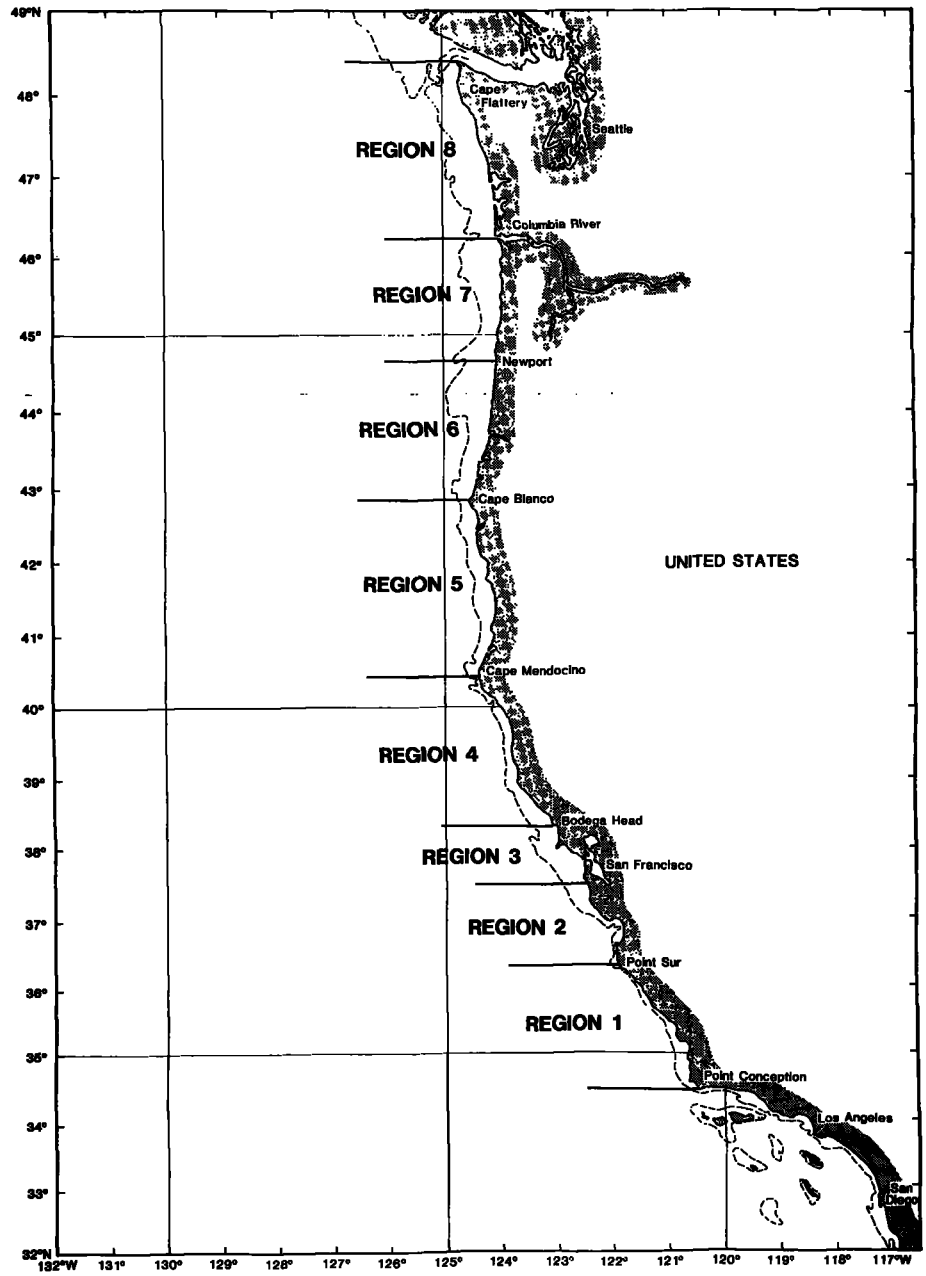

FIGURE 2.—Geographic regions used as strata in density estimation.

by adding all appropriate transect segments to a linear array and dividing that array into 10 equal parts.

When paired tests were not applicable, nonparametric ANOVA models were used. For simple comparisons, the Kruskal-Wallis single-factor analysis of variance was used (Kruskal and Wallis 1952). For two-way comparisons, we used a two-factor extension of the Kruskal-Wallis test (Scheirer et al. 1976). For both tests, three replicate measures of density were created for each cell by randomly assigning transect segments as replicate 1, 2, or 3.

A principal assumption of strip transect methods is that all individuals within the designated strip are counted. Assuming that the fraction of diving animals does not vary with sighting conditions, any effect of sighting conditions on apparent density is likely due to missed animals. In any instance where we show that poorer sighting conditions result in a significant decrease in apparent density (one-tailed for paired tests, two-tailed for ANOVA tests), we eliminate the category of sighting conditions which resulted in that lower estimate. If it is not possible to predict which category would be worse a priori in paired tests (e.g., right swath vs. left), two-tailed probabilities are used. Although we cannot be sure of eliminating all biases using these methods, this pattern of data paring should avoid much of the bias due to missed animals.

RESULTS

In 1984, 247 groups of harbor porpoise (680 individuals) were seen within transect strips which covered a linear distance of 5,763 km. In 1985, we saw 119 groups (384 individuals) in surveys of 3,715 km. Mean group sizes were 2.75 and 3.23 individuals, respectively, for 1984 and 1985. For 1984, the relative frequencies of individuals seen within the inside and outside swaths are illustrated in Figure 1. For 1985, the perpendicular distances from the trackline to the animals were calculated from declination angles, and the relative distribution of sightings is shown in Figure 1 as a function of perpendicular distance.

Inside vs. Outside Swath

For 1984 data, only the inside swaths were used, but for 1985 both inside and outside swaths were considered for density estimation. For 1985, we tested whether the density in the inside swaths was greater than the density of the outside swaths. We only considered cases when the water surface penetration codes were equal in both the inside and outside swaths. Data for inside and outside were thus paired, with all other sighting factors equal. For 1985, the density in the inside was greater (0.09 vs. 0.06 porpoise/km^2), but this difference was not significant ($P > 0.10$).

Surface Penetration

Observers used a subjective coding system to describe their ability to see through the sea surface. Cloud cover, haze, and water turbidity contributed to poor surface penetration. In 1984, observers used codes to indicate good and poor conditions; in 1985, observers used codes for excellent, good, and poor. There were frequent cases when observers recorded different codes for the inside swaths on opposite sides of the plane; hence, paired tests were again appropriate. For 1984, we tested whether density in the "good" category was higher than density in the "poor" category. When surface penetration was different in the inside swaths on opposite sides of the plane, mean density in the "good" category was higher than in the "poor" category (0.16 vs. 0.12 porpoise/km^2), but this difference was not significant ($P > 0.25$). For 1985, no tests were necessary because the mean density in "excellent" category was lower than in the "good" category, and likewise, density in the "good" was lower than in the "poor" category. All categories of water surface penetration were included in subsequent analyses.

Effects Due to Observers and Side of the Plane

Sightings were classified based on which observer made the sighting and on whether the sighting was on the inshore or offshore side of the aircraft. In fact, these two classifications were confounded in 1985 because the two principal observers were situated on the same sides of the aircraft for most of this survey. Effects of these classifications on density estimation were considered together. Survey teams were defined as pairs of observers who worked together. There were two such teams for 1984 and three for 1985 (Table 1). Only one of the teams in 1985 had sufficient numbers of sightings to be considered here. Statistical tests were based on paired cases during which both members of the sighting team were searching.

For 1984, porpoise density on the offshore side of the airplanes was greater than on the inshore side for both team A and team B (Table 2). The difference in density estimates between observers was less than the difference between inshore and off-

TABLE 2.—Relative harbor porpoise densities (km^{-2}) for teams of observers. Density estimates are stratified by inshore and offshore sides of the aircraft and by individual observers.

Observer team	Inshore	Offshore	Observer 1	Observer 2
A	0.275	0.425	0.320	0.380
B	0.168	0.244	0.232	0.179
D	0.281	0.164	0.300	0.146

shore (Table 2), and neither was statistically significant. For 1985, the opposite was seen; the density on the inshore side was greater than on the offshore side and this difference was less than the difference between observers (Table 2), but again, neither difference was statistically significant. In 1984, both observers had previous experience doing aerial surveys, but in 1985, the observer with the lower density estimates had no previous experience in cetacean surveys. Experience may be a factor in density estimates from strip transects, but since the inexperienced observer was always on the same side of the plane, it was not possible to test this with a factorial design.

Area and Sea State

Analysis of research vessel data (Barlow 1988) indicated two geographic regions in California with low porpoise density (regions 1 and 3 in Figure 2). We tested whether density observed from aircraft are also lower in these areas. Because observation conditions may have differed in the two areas, we included sea state as a second factor in a two-way ANOVA. Mean values are presented in Table 3. For 1984, three categories of sea state were used: Beaufort 0 & 1, Beaufort 2, and Beaufort 3 and greater. The effect due to area was significant ($P < 0.001$), with the area that showed low density in the ship surveys also showing lower density in the aerial survey. For 1985, only the first two categories of sea state were used due to insufficient data at Beaufort 3 and greater. Again the effect of area was significant ($P < 0.025$), and the same trends were seen. In neither case were the effects of sea state or the interaction effects significant. To eliminate area effects from confounding statistical results, only data for the larger, high-density area were included in subsequent tests. The low-density area was included in later estimates of overall harbor porpoise density.

TABLE 3.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of area and sea state. Low-density areas refer to two regions in California that were found to have much lower than average density in previous ship surveys (see text). High-density areas include all other regions. Only inside swaths were included. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

Beaufort sea state	1984 survey		1985 survey	
	Low-density area	High-density area	Low-density area	High-density area
0 & 1	0.027 (183)	0.579 (264)	0.089 (124)	0.762 (126)
2	0.081 (308)	0.312 (1012)	0.089 (214)	0.183 (425)
3+	0.102 (79)	0.191 (252)	[0.000] (28)	[0.049] (566)

Sea State and Cloud Cover

Both sea state and cloud cover can affect sighting conditions. Because both are affected by local weather, the effects of these are likely to be confounded. These two factors were therefore tested simultaneously in a two-way ANOVA. We considered only the inside swath and excluded the two low-density regions. We used the same sea state categories as above. The sky was categorized as clear if cloud cover was <25% and cloudy if >25%. Mean porpoise densities for each category are given in Table 4. It was necessary to exclude the Beaufort 0 & 1 category for 1985 because only 52 km were surveyed in cloudy conditions for these sea states. The effect due to cloud cover was significant for 1984 ($P < 0.025$) and 1985 ($P < 0.05$). The effect of sea state and the interaction effect of sea state and cloud cover were not significant for either survey ($P > 0.10$). Transect segments with >25% cloud cover were excluded from subsequent analyses.

TABLE 4.—Uncorrected harbor porpoise densities (km^{-2}) for the two-way comparison of sea state and cloud cover. Clear refers to <25% cloud cover, and cloudy refers to >25%. Data include only inside swaths in high-density areas. Numbers in parentheses refer to area (km^2) surveyed under the given condition. Densities in brackets were excluded from two-way comparisons due to the small area covered in one cell.

Beaufort sea state	1984 survey		1985 survey	
	Clear	Cloudy	Clear	Cloudy
0 & 1	1.340 (81)	0.240 (183)	[0.832] (115)	[0.000] (11)
2	0.371 (572)	0.236 (440)	0.271 (232)	0.078 (193)
3+	0.266 (162)	0.056 (90)	0.088 (272)	0.014 (294)

Sea State

The effect of sea state was tested alone using only the transect segments which occurred under clear skies (<25% cloud cover) and within the high-density areas. For 1984, only the inside swath was included.

For 1985, both inside and outside swaths were included. As in previous stratifications, apparent density clearly decreased with increasing sea state (Table 5). This effect was significant for surveys in both 1984 ($P < 0.05$) and 1985 ($P < 0.005$). Transect segments surveyed during sea states of 2 or greater were excluded in subsequent analyses.

TABLE 5.—Uncorrected harbor porpoise densities (km^{-2}) for the stratification based on sea state. Data include only high-density areas surveyed when cloud cover was <25%. Data for 1984 include inside swaths only; data for 1985 include inside and outside swaths. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Beaufort sea state	1984 survey	1985 survey
0 & 1	1.340 (81)	0.807 (234)
2	0.371 (572)	0.193 (471)
3+	0.266 (162)	0.058 (553)

Between Survey Differences

We considered the 1984 survey and the 1985 surveys at 0.61 km and 1.85 km from shore as three independent estimates of harbor porpoise density. Because apparent density was shown to vary greatly with sighting conditions and because sighting conditions varied between surveys, it was necessary to compare these three under similar conditions.

The highest (and presumably least biased) densities were obtained when sea state was Beaufort 0 & 1 and when cloud cover was <25%. Between survey comparisons under these conditions are given in Table 6 for the eight geographic regions given in Figure 2. For 1985, there were no transect segments at 0.61 km from shore under the conditions Beaufort 0 & 1 and clear skies. For 1984, only three regions contained more than 10 km^2 of searching effort at 0.61 km from shore. For 1985, only four areas had any searching effort at 1.85 km from shore. The only direct density comparisons with reasonable sample sizes are for region 1 (0.000 vs. 0.048 porpoise/km^2) and region 3 (0.111 vs. 0.110 porpoise/km^2) (respectively for 1984 and 1985). The densities for all regions pooled (0.671 and 0.510 porpoise/km^2) are similar, but because of the small sample size and geographic variation in sampling, a statistical test of this difference is meaningless.

In comparing surveys, sample size and regional coverage improved slightly when Beaufort 2 was considered (still allowing a maximum of 25% cloud cover) (Table 7). For 1984, coverage was relatively complete in all regions. For 1985, coverage at 0.61 km from shore was limited to regions 2–4, and coverage at 1.85 km was limited to regions 1–5. Comparing the two surveys in 1985, distance from shore made little difference in overall density for all regions combined, and neither survey had consistently higher values than the other. Comparing the 1984 survey to the two 1985 surveys, the former had a higher overall density for all regions combined, but again this difference was not consistent among regions. Sample size and regional coverage were again too poor for meaningful statistical tests.

TABLE 6.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 0 & 1 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (43)	— (0)	0.048 (103)
2	0.000 (1)	— (0)	0.609 (51)
3	0.111 (45)	— (0)	0.110 (55)
4	0.953 (6)	— (0)	0.862 (183)
5	1.120 (9)	— (0)	— (0)
6	1.374 (64)	— (0)	— (0)
7	5.745 (1)	— (0)	— (0)
8	— (0)	— (0)	— (0)
All regions	0.671 (170)	— (0)	0.510 (392)

Ventilation Patterns

Harbor porpoise did not appear to react to the helicopter during aerial observations; they were visible throughout a surfacing series and were not visible during dives. Knowing this, we were able to use data on surfacing series and dive times to determine the fraction of time harbor porpoise would be visible from the air. Data on ventilation patterns

were available from the helicopter study in California (13 groups were observed, mean group size was 2.7), the Oregon shore observations (11 groups, mean group size was 4.2), and a previous shore study in Glacier Bay, AK (28 solitary individuals). The mean times spent in surfacing series were 34.2, 24.6, and 30.0 seconds (respectively for the three studies). The corresponding mean dive times did not differ significantly between study sites ($P > 0.05$ using pairwise t-tests). Using the pooled data set ($n = 52$), the mean time spent in a surfacing series was 30.02 seconds (SE = 1.95) and the mean time spent in a dive was 95.81 seconds (SE = 5.32). The percentage of time spent at the surface is 23.9%.

Average and Adjusted Density Estimates

Harbor porpoise densities under optimal conditions (Beaufort 0 & 1 and <25% cloud cover) were averaged for the two surveys, weighting by transect length (Table 8). Given an average survey speed of 160 km/h and assuming that the window for harbor porpoise observation is 400 m long, the time window during which a point would be visible is 9.0 seconds. Using this estimate and the surface and dive times estimated above, the probability that a porpoise will be seen is estimated as 0.310 from Equation (2). An instantaneous count would therefore underestimate porpoise abundance by a factor of 3.2. Average values were therefore multiplied by this factor (Table 8).

TABLE 7.—Uncorrected harbor porpoise densities (km^{-2}) in eight geographic regions surveyed during Beaufort 2 conditions. Data for 1984 are based on inside swaths of transects flown 0.61 km from the coast. Data for 1985 are based on inside and outside swaths of transects flown at 0.61 and 1.85 km from the coast. Only those segments surveyed when cloud cover was <25% are included. Numbers in parentheses refer to area (km^2) surveyed under the given condition.

Geographic region	1984 survey density 0.61 km	1985 survey density 0.61 km	1985 survey density 1.85 km
1	0.000 (107)	— (0)	0.184 (103)
2	0.092 (109)	0.102 (59)	0.103 (68)
3	0.196 (117)	0.062 (48)	0.287 (52)
4	0.562 (180)	0.282 (110)	0.070 (57)
5	0.489 (119)	0.459 (6)	0.234 (171)
6	0.439 (57)	— (0)	— (0)
7	0.114 (70)	— (0)	— (0)
8	0.268 (37)	— (0)	— (0)
All regions	0.295 (796)	0.192 (224)	0.188 (452)

DISCUSSION

Results indicate that sighting conditions must be very good in order to estimate harbor porpoise abundance from aerial strip transects. Both sea state and cloud cover had very large and significant effects on apparent density. Limiting observations to the best categories of sea state (Beaufort 0 & 1) and cloud cover (<25%) can be used to minimize the bias due to missed animals. These conditions are, however, rare and only occurred during 5.3% and 10.3% of the transects in 1984 and 1985. The actual occurrence of these conditions is even more rare if one considers flights that were cancelled due to bad weather.

The effects on sea state and cloud cover on sighting conditions were predicted by observers before analysis of survey data was begun. Most harbor porpoise were first seen when submerged a small distance below the surface. Surfacings were relatively inconspicuous to aerial observers and were not an important cue in sighting porpoise. Both sea state and cloud cover affect the ability of observers to see through the water's surface and to spot submerged animals. Increasing sea state causes more refraction of light at the water's surface, increases glit-

TABLE 8.—Harbor porpoise densities (km^{-2}) in eight geographic regions from a) a weighted average of uncorrected estimates from 1984 and 1985 aerial surveys, b) the same average adjusted by a factor of 3.2 to account for submerged porpoise that were missed by aerial observers, and c) a weighted average for the 1984 and 1985 ship surveys. Aerial estimates are based on observations made under conditions of Beaufort 0 & 1 and with <25% cloud cover. Ship estimates include Beaufort sea states of 0, 1, and 2.

Geographic region	Area surveyed (km^2)	Aerial estimates		Research vessel estimates
		Uncorrected a	Corrected b	c
1	146	0.03	0.10	0.05
2	1	—	—	0.66
3	100	0.11	0.35	0.04
4	189	0.86	2.75	3.68
5	9	1.12	3.58	1.18
6	64	1.37	4.38	2.88
7	1	—	—	3.43
8	0	—	—	1.42
All regions	562	0.559	1.79	1.73

tery reflection of sunlight, and causes whitecaps which obscure subsurface observation. Cloud cover decreases penetration of sunlight into the sea and causes its surface to appear dark and glazed. It is therefore not surprising that calm seas and clear skies result in higher apparent densities.

It is more surprising that apparent density did not vary with observer's subjective appraisal of surface penetration. This may have been because surface penetration was only tested in paired cases for which sea state and cloud cover were identical. In these cases, differences in surface penetration may have been due primarily to subjective differences in the way individual observers were coding it. If all cases are considered, surface penetration is very highly correlated with sea state and cloud cover and probably could be used as an alternative measure of sighting conditions. We prefer, however, to use sea state and cloud cover because their measure is less subjective than surface penetration and could more easily be used by other researchers.

Missed Animals

A principal assumption of strip transect methods is that all individuals within the strip are counted. We cannot necessarily meet this assumption just by eliminating the categories of sighting conditions with significantly lower density. In fact, it is possible that this method of selectively eliminating data could overestimate density by eliminating a category of sighting conditions which (by random chance) had a significantly lower density. We do not believe that this is likely in the cases of sea state or cloud cover because the trends were the same for both surveys and because the categories that were eliminated were judged a priori as being poorer sighting conditions. We believe that porpoise density is more likely underestimated due to missed animals. Kraus et al. (1983) found that observers in aircraft saw only 14% of the harbor porpoise groups known to be present based on shore-based observations. Missed animals may include some individuals that were near the surface and visible but were not seen, as well as others that were diving and were too deep to be seen.

We infer that some near-surface animals were missed based on three reasons. First, apparent density decreased with increasing sea state and cloud cover, hence near-surface animals must be missed in (at least) the poorer conditions. (An alternative explanation is that porpoise spend less time near the surface when sighting conditions are poor.) Second, of the two principal observers in 1985, the less experienced observer may have missed more porpoise. Third, in five instances in 1984 and one instance in 1985, the data recorder saw harbor porpoise in the inside swath that were missed by the observer. In three of these cases, conditions were Beaufort 1 with <25% cloud cover. Recorders searched only occasionally as conditions permitted, so it is not possible to use these data to quantify how many near-surface animals were missed under good conditions.

Based on behavioral observations, we can also be certain that some harbor porpoise are missed because they are too deep to be seen. Water visibility was typically only 2–5 m during the surveys. Aerial observers have seen harbor porpoise dive out of view during the passing of the plane or while circling. Harbor porpoise were not visible from the helicopter during dives, even in very calm water. Some fraction of porpoise must be missed because they are too deep to be seen.

We have tried to account for the fraction of diving animals by dividing density estimates by the fraction of time harbor porpoise are known to be near the surface (i.e., within surfacing series). Uncorrected estimates of harbor porpoise density are based on the assumption that porpoise are never too deep to be seen; this undoubtedly results in an underestimate of porpoise density. Our method of adjusted estimates of porpoise density assumes that, when diving, porpoise are always too deep to be seen; this has been corroborated by helicopter observations. The latter estimate should therefore be closer to the true value of porpoise density (if biases due to other factors have been eliminated).

Offshore Distribution of Harbor Porpoise

In 1985, aerial transects were flown at 0.61 and 1.85 km from the shore. The latter value was chosen to correspond approximately to the ship transects along the 10-fathom (18.3 m) isobath. The intent was to directly compare aerial estimates of density to estimates made from ships at the same distance from shore (considered below) and to provide a means to extrapolate ship estimates to regions that were too shallow to survey by ship. In regard to the latter, we wish to know whether harbor porpoise density at 0.61 km from shore is different from that at 1.85 km.

In 1985, surveys at 0.61 km were never flown under good sighting conditions (Beaufort 0 & 1 and <25% cloud cover), so direct comparisons between 0.61 and 1.85 km are not possible. Considering only the best category of sighting conditions, it is possi-

ble to compare 1985 transects at 1.85 km with 1984 transects at 0.61 km in geographic regions 1 and 3 (Table 6). Sample sizes are very small, but densities are roughly comparable (0.070 vs. 0.057, respectively for 1.85 and 0.61 km from shore). Sample sizes in 1985 can be increased if Beaufort 2 is considered instead of Beaufort 0 & 1 (still with <25% cloud cover). Based on geographic regions 1 through 5, porpoise densities are virtually identical at 1.85 and 0.61 km from shore (0.188 vs. 0.192, respectively, Table 7).

In a preliminary model of harbor porpoise depth distribution, Barlow (1988) hypothesized that harbor porpoise density is constant from the shore to the 75 m isobath. Ship data did not, however, include any transects inshore of 18.3 m depth. In this shallow area, the model was not based on any data. Although sparse, data from aerial surveys show that densities are similar in areas that were surveyed by ship (1.85 km from shore) and in areas that were too shallow to be surveyed by ship (0.61 km from shore). These data are consistent with the model proposed by Barlow.

Comparison of Ship and Aerial Density Estimates

Estimates of harbor porpoise density from 1984 to 1985 ship surveys (Barlow 1988) can be compared with adjusted and unadjusted estimates from the aerial surveys (Table 8). The overall density for all regions is higher for the ship surveys than for the unadjusted aerial. Adjusted estimates from the aerial surveys are very close to the overall estimates from ship surveys.

Previous comparisons have been made of sighting efficiency from aerial and surface vessel platforms (Kraus et al. 1983). They found that observers on boats saw 52% of the harbor porpoise groups seen by shore-based observers, whereas aerial observers saw only 14%. Based on this, density from aerial surveys might be expected to be only 27% of that from ship surveys. In the present study, unadjusted density based on aerial surveys is 32% of the density from ship surveys. The two studies are not directly comparable, however. Weather conditions are not reported by Kraus et al. (1983) and may have included less than optimal sighting conditions. It should be noted that the fraction of harbor porpoise groups seen by aerial observers in their study (14%) is even lower than the fraction of harbor porpoise we assumed would be in surfacing series and hence near the surface (23.9%). It is possible that behavioral differences between harbor porpoise from the two coasts (such as travelling or behavior mode "A" noted by Watson and Gaskin (1983)) could account for some of the differences noted above.

Estimates based on ship surveys cannot, of course, be considered the true density of harbor porpoise. The overall estimate based on ship surveys is relatively imprecise (C.V. = 49%) and may be biased (Barlow 1988). The ship survey estimate is, however, superior to current estimates from aircraft for several reasons. Line transect methods were used on the ship surveys, and the principal assumption of this method (that 100% of the animals in the immediate vicinity of the trackline are seen) is more easily met than the comparable strip transect assumption (that 100% of the animals within a strip are seen). Acceptable sighting conditions for ship surveys included Beaufort 0 & 1, and 2 and were not restricted by cloud cover (Barlow 1988). This allowed more complete geographic coverage than did aerial surveys. Also, the ship travelled much slower than the aircraft (10 knots vs. 80–90 knots), thus the probability of missing a diving individual was much less. Barlow (1988) calculated that diving animals located near the trackline would be missed by observers on ships only if dive times exceeded 2 minutes. Finally, estimates of the correction factor to account for submerged animals is relatively imprecise. Additional observations on ventilation patterns may allow further refinements in density estimates based on aerial surveys.

RECOMMENDATIONS

The design of future surveys for harbor porpoise could be improved based on the results obtained from our aerial surveys. We found that sighting conditions deteriorated rapidly with both increasing cloud cover and rougher sea states. To the extent that is possible, aerial surveys for harbor porpoise should only occur on clear days with little wind. Observations made by the data recorders indicate that some harbor porpoise will be missed even in good sighting conditions. If strip transects are used, experiments with two independent teams of observers searching at the same time could be used to quantify the fraction of animals that are missed by using just one team. Given that fewer harbor porpoise were seen between 400 and 500 m of the track line, we also suggest that, when surveying at 213 m altitude, the strip widths should be decreased to only include the area between 100 and 400 m.

We believe, however, that the problem of missing harbor porpoise could be reduced if line transect methods were used in place of strip transects. Line

transect methods assume that 100% of all animals are seen directly along the trackline and use statistical techniques to estimate the number of animals that are missed as a function of the distance from this trackline. Line transects would require use of an aircraft with unobstructed downward visibility through a belly window and use of a third observer who could view animals directly under the aircraft.

Harbor porpoise are now known to occur further from the shoreline than was believed at the beginning of this study (Barlow 1988). In future surveys, transect lines should be placed so as to cover a greater fraction of the harbor porpoise habitat.

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EVALUATION OF VARIABILITY IN SABLEFISH, *ANOPLOPOMA FIMBRIA*, ABUNDANCE INDICES IN THE GULF OF ALASKA USING THE BOOTSTRAP METHOD

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ABSTRACT

Relative population numbers (RPN's) and length compositions were computed for sablefish, *Anoplopoma fimbria*, in the Gulf of Alaska from the results of the Japan-United States cooperative longline survey from 1979 to 1986. A statistical evaluation of annual changes in the RPN's using the bootstrap method is demonstrated and showed that sablefish abundance increased significantly from 1979 to 1986, an increase likely due to recruitment of two strong year classes. The effect of missing data on the bootstrap calculations was examined and found to be negligible.

Early in this century, United States and Canadian fishermen began harvesting sablefish, *Anoplopoma fimbria*, in nearshore waters from California north to southeastern Alaska, but sablefish were not heavily exploited until Japanese longline vessels began fishing in the Bering Sea in 1958. Japanese catches off both the U.S. and Canadian coasts rose dramatically in the following two decades. After passage of the Fishery Conservation and Management Act, foreign catches were reduced and the domestic allocation was increased. The domestic catch eventually increased nearly fivefold, thereby replacing the foreign fishery, and in 1985, sablefish in the Gulf of Alaska were harvested entirely by domestic fishermen.

Before the reduction of the foreign fishery, information on sablefish abundance consisted of statistics on catch per unit effort from the Japanese longline fishery. In 1978, the Fisheries Agency of Japan and the U.S. National Marine Fisheries Service (NMFS) began a cooperative longline survey along the continental slope of Alaska to assess the abundance of sablefish and Pacific cod, *Gadus macrocephalus*. The survey, conducted annually, has provided eight consecutive years (1979–86) of data for the Gulf of Alaska, seven years (1980–86) of data for the Aleutian region, and five years (1982–86) of data for the eastern Bering Sea. The first year of the survey, 1978, was experimental.

Relative population numbers (RPN's) and length compositions from the longline survey results from 1979 to 1985 have been estimated previously by Sasaki (1986). In this study, the observed increase in the RPN's for sablefish in the Gulf of Alaska is evaluated statistically and an explanation of the probable source of the increase is discussed.

Statistical analysis of the survey results is based on the bootstrap method (Efron 1982; Efron and Gong 1983). This method is a relatively new statistical procedure that has been little used in fisheries analysis. Thus, this paper also demonstrates an application of the bootstrap method to statistical evaluation of fishery survey data.

SURVEY METHODS

The Gulf of Alaska portion of the Japan-U.S. cooperative longline survey, conducted annually each summer from 1979 to 1986, covered five International North Pacific Fisheries Commission (INPFC) statistical areas: Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern (Fig. 1). One of a total of 47 stations each ranging in depth from about 100 to 1,000 m was sampled daily by longline. The longline was 16 km long and consisted of 160 hachis (the Japanese word for "skate" or length of longline); each hachi was 100 m long and consisted of 45 hooks baited with squid. Soak time, the time between setting and retrieval, varied from 3 hours at the beginning of the longline gear to 7 or 8 hours at its end. The depth at which the fish were caught was estimated by measuring the depth of water under the vessel with an echo sounder every fifth hachi. The fish caught were tallied by species and hachi as the longline was brought aboard, then they were weighed and their length was measured. Most

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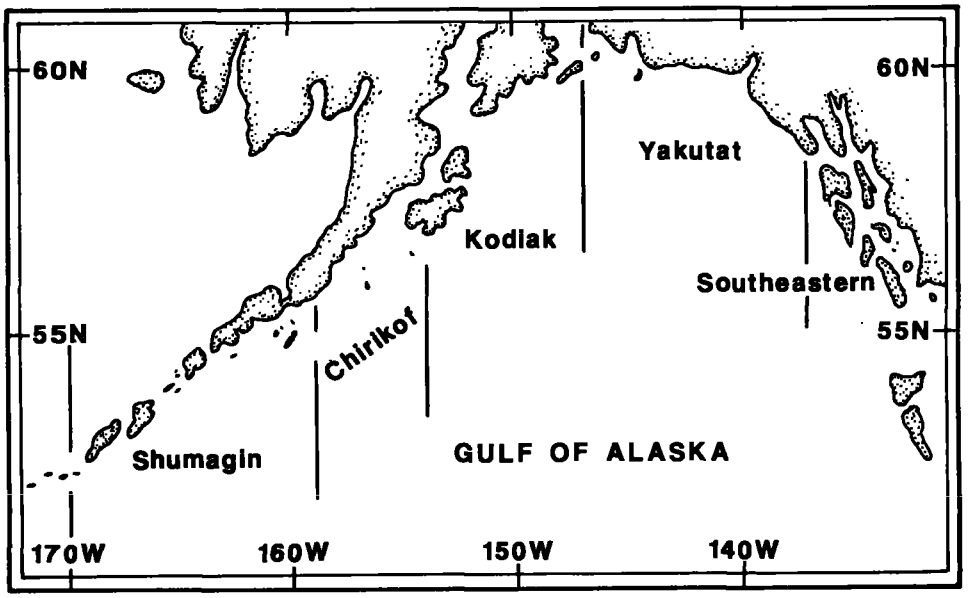

FIGURE 1.—International North Pacific Fisheries Commission statistical areas sampled during the Gulf of Alaska portion of the Japan-U.S. cooperative longline survey, 1979–86.

sablefish were sexed, some were tagged and released, and others were sampled for otoliths and scales. Detailed survey methods are described in Sasaki et al. (1983).

STATISTICAL METHODS

The catch data were stratified because of differences in the catch rate by depth. Assignment of the

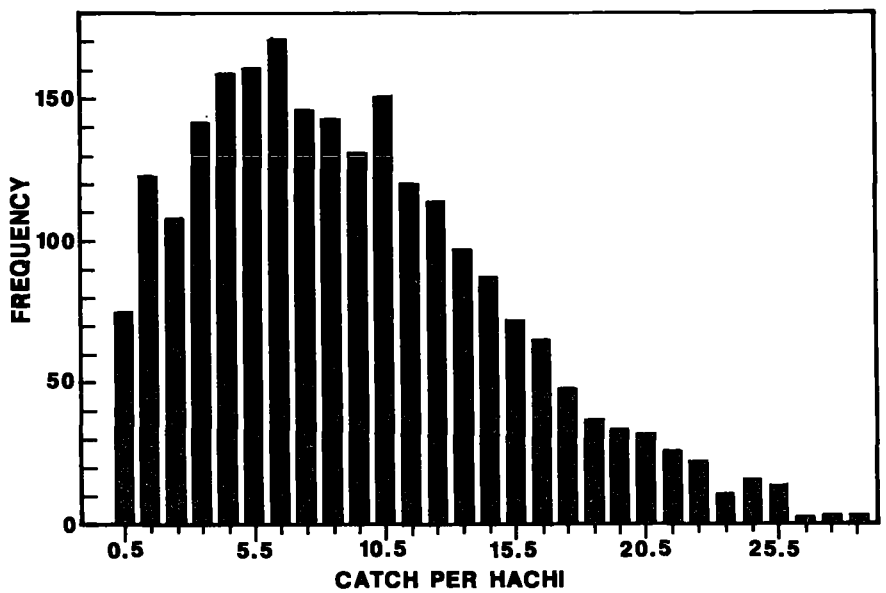

FIGURE 2.—Frequency distribution of sablefish catch per hachi (numbers) by year, station, and strata, 1979–86.

catch data to a stratum was based on the recorded depth of every fifth hachi or the interpolated depth of each of the intervening four hachis. The number of strata totaled nine, with the first stratum representing 101–200 m, the second representing 201–300 m, and so on. A catch per hachi value was calculated for each stratum of a station (Fig. 2), and the resultant values within each statistical area were averaged.

Not all strata were sampled at each station and as a result, sometimes no stations were sampled within certain strata (Table 1). Although not sampled one year, these strata generally were sampled the previous year, because of slight annual differences in the depths sampled at each station. Catch per hachi values $CPUE_{i,j}$ were estimated for stations within the unsampled strata from the catch per hachi values for sampled stations from the previous year and the annual change in the catch per hachi values in the adjacent stratum. For each station:

$$CPUE_{i,j} = CPUE_{i-1,j} * CPUE_{i,j'}/CPUE_{i-1,j'}$$

where i = year, j = stratum, and j' = the adjacent stratum. Catch per hachi values were estimated only for stations within unsampled strata. If one or more stations within a stratum were sampled, then no catch per hachi values were estimated for the unsampled stations. The effect of these missing values on the survey results will be discussed later.

Relative population numbers were calculated from the catch per hachi values to index annual changes in sablefish abundance. As in Sasaki (1985), the average catch per hachi was multiplied by the areal size of each stratum and statistical area to calculate an RPN for each stratum and statistical area. The areal sizes used to calculate the RPN's are for the continental slope only (Table 2), which corresponds to the area covered by the survey. The resultant RPN's were summed across strata to calculate an RPN for each statistical area, and these RPN's were summed

TABLE 1.—Number of stations sampled by year, INPFC area, and depth during the Japan-U.S. cooperative longline survey, 1979–86.

		INPFC statistical area							INPFC statistical area				
Year	Depth (m)	Shumagin	Chirikof	Kodiak	Yakutat	Southeast	Year	Depth (m)	Shumagin	Chirikof	Kodiak	Yakutat	Southeast
1979	101–200	7	4	6	6	2	1983	101–200	9	5	7	8	3
	201–300	7	5	7	10	5		201–300	10	6	9	11	9
	301–400	7	5	8	11	6		301–400	10	5	9	11	8
	401–500	7	5	9	11	6		401–500	10	6	9	11	8
	501–600	6	4	9	11	6		501–600	10	5	9	11	8
	601–700	6	4	8	11	5		601–700	9	5	9	11	7
	701–800	6	4	7	11	5		701–800	8	4	8	11	7
	801–900	5	1	4	9	4		801–900	5	4	4	10	7
	901–1,000	4	1	2	4	1		901–1,000	2	0	1	5	2
1980	101–200	9	5	8	7	4	1984	101–200	10	7	7	8	2
	201–300	10	6	8	10	6		201–300	10	7	9	11	9
	301–400	10	6	8	10	8		301–400	10	6	9	11	8
	401–500	10	6	9	10	8		401–500	10	6	9	11	8
	501–600	10	5	9	10	7		501–600	10	5	9	11	8
	601–700	9	5	9	9	7		601–700	8	5	8	11	8
	701–800	6	4	8	9	7		701–800	7	5	6	10	8
	801–900	6	2	3	7	4		801–900	3	0	3	7	5
	901–1,000	5	1	2	6	1		901–1,000	0	0	0	6	1
1981	101–200	9	6	7	8	1	1985	101–200	9	6	6	7	1
	201–300	10	6	9	11	9		201–300	10	7	8	11	9
	301–400	10	6	9	11	9		301–400	10	6	9	11	8
	401–500	10	6	9	11	9		401–500	10	6	9	11	7
	501–600	10	6	9	11	9		501–600	10	6	9	11	8
	601–700	9	4	9	11	9		601–700	9	5	9	11	8
	701–800	7	2	7	11	9		701–800	7	4	9	10	8
	801–900	6	1	5	7	7		801–900	4	4	4	11	6
	901–1,000	2	0	1	2	1		901–1,000	0	0	0	5	2
1982	101–200	9	5	7	10	4	1986	101–200	9	5	7	7	2
	201–300	9	6	9	11	9		201–300	10	6	9	11	9
	301–400	10	5	9	11	8		301–400	10	6	9	11	8
	401–500	10	6	9	11	8		401–500	10	6	9	11	8
	501–600	10	5	9	11	8		501–600	10	6	9	11	8
	601–700	10	5	9	11	8		601–700	10	4	9	11	8
	701–800	9	4	8	11	7		701–800	10	3	8	11	8
	801–900	7	4	6	9	6		801–900	5	2	7	11	8
	901–1,000	3	3	5	8	3		901–1,000	1	1	3	5	1

TABLE 2.—Slope area sizes (km^2).

Depth (m)	Slope area (km^2)[1]				
	Shumagin	Chirikof	Kodiak	Yakutat	Southeast
201–400	4,001	2,350	3,106	2,988	1,781
401–600	2,269	1,766	2,255	1,666	822
601–800	1,629	1,955	1,923	1,470	1,006
801–1,000	1,248	2,012	2,296	1,489	1,165
201–1,000	9,147	8,083	9,580	7,613	4,774

[1]Shumagin, Chirikof, and Kodiak areas and Yakutat area from long. 147–144°W; data from E. Brown (NWAFC Seattle Laboratory, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, WA 98115, pers. commun. December 1985). Yakutat area from long. 144–137°W. and Southeastern area; data from R. Haight (NWAFC Auke Bay Laboratory, NMFS, NOAA, P.O. Box 210155, Auke Bay, AK 99821, pers. commun. 1986).

across statistical areas to calculate an RPN for the Gulf of Alaska. The bootstrap method (Efron 1982; Efron and Gong 1983) then was applied to the resultant RPN's to test the statistical significance of annual changes in the RPN's.

The bootstrap method is a nonparametric statistical procedure based on Monte Carlo methods (see Shreider [1966] for a description of Monte Carlo methods). The bootstrap method is a new technique not common in the fisheries and ecology literature, but examples of its application to survey design and biomass estimation can be found in Kimura and Balsiger (1985) and Haslett and Wear (1985), respectively. In addition, Rao and Wu (1984) proved the applicability of the bootstrap method to stratified sampling, which is the sampling method used in the longline survey. The bootstrap method is useful when parametric assumptions are difficult to justify; no parametric estimate is readily available for the accuracy of a statistic, e.g., a sample median; or the procedure to compute the statistic of interest is complicated. Simply described, the bootstrap method works as follows: Given the observed data set $<X_1,X_2,\ldots,X_n>$, the sample $<X_1^*,X_2^*,\ldots,X_n^*>$ is drawn by independent random sampling with replacement from the observed data set and the desired statistic (e.g., a median) is computed from the sample. The resultant statistic is termed the bootstrap replicate. In the next step, the sample is drawn and the bootstrap replicate is computed some large number B times. The resultant B bootstrap replicates form the bootstrap distribution. An estimate of the accuracy of the median, a standard error, then can be calculated from the bootstrap distribution by standard methods.

In this study, we used the bootstrap method to test the null hypothesis that the difference $RPN_{i',k} - RPN_{i,k} = 0$, for any $RPN_{i,k'}$, where i = year (1979–86), i' = any subsequent year, and k = statistical area (Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern). The bootstrap method was used because parametric assumptions are difficult to justify for the longline survey data and the procedure to compute the statistic of interest, the variance of the RPN, is tedious and error prone. In our application of the bootstrap method, stations were randomly sampled with replacement within each area. A value denoted $RPN_{i,k}^*$ was computed from the catch per hachi values of the sampled stations by the method of RPN calculation described previously. Stations then were sampled with replacement from year i' within each area, a second value denoted $RPN_{i',k}^*$ was computed, and the difference $RPN_{i',k}^* - RPN_{i,k}^*$ was found. Sampling with replacement from the 2 years and the computation of the difference were repeated 1,000 times producing a bootstrap distribution of 1,000 differences.

Efron and Tibshirani (1986) outlined three methods for setting an approximate confidence interval from a bootstrap distribution for a statistic of interest, here the difference $RPN_{i',k} - RPN_{i,k}$. Use of the simplest method, the percentile method, is considered correct if the bootstrap distribution of the statistic of interest is described by a normal distribution (Efron and Tibshirani 1986). The normality of the bootstrap distribution for the difference was tested using the D'Agostino D Test (D'Agostino and Stephens 1986) and found to be normal, thus justifying the use of the percentile method. The statistical significance of the difference $RPN_{i',k} - RPN_{i,k}$ then was evaluated by the following criteria. If the 95% confidence interval for the difference did not include zero, then the null hypothesis was rejected, the annual change in the RPN was considered statistically significant, and the change in sablefish abundance was considered real. Conversely, if the 95% confidence interval for the difference included zero, the null hypothesis was accepted and the change in sablefish abundance was not considered significant.

RESULTS

The RPN for the Gulf of Alaska increased 111% from 1979 to 1986 (Fig. 3). The 95% confidence interval for this increase did not include zero and therefore was judged statistically significant (alpha = 0.05; Table 3), showing that the difference was not due to random error in the survey and that sablefish abundance in the Gulf of Alaska has increased markedly since 1979. The difference consists of significant increases from 1980 to 1981, 1981

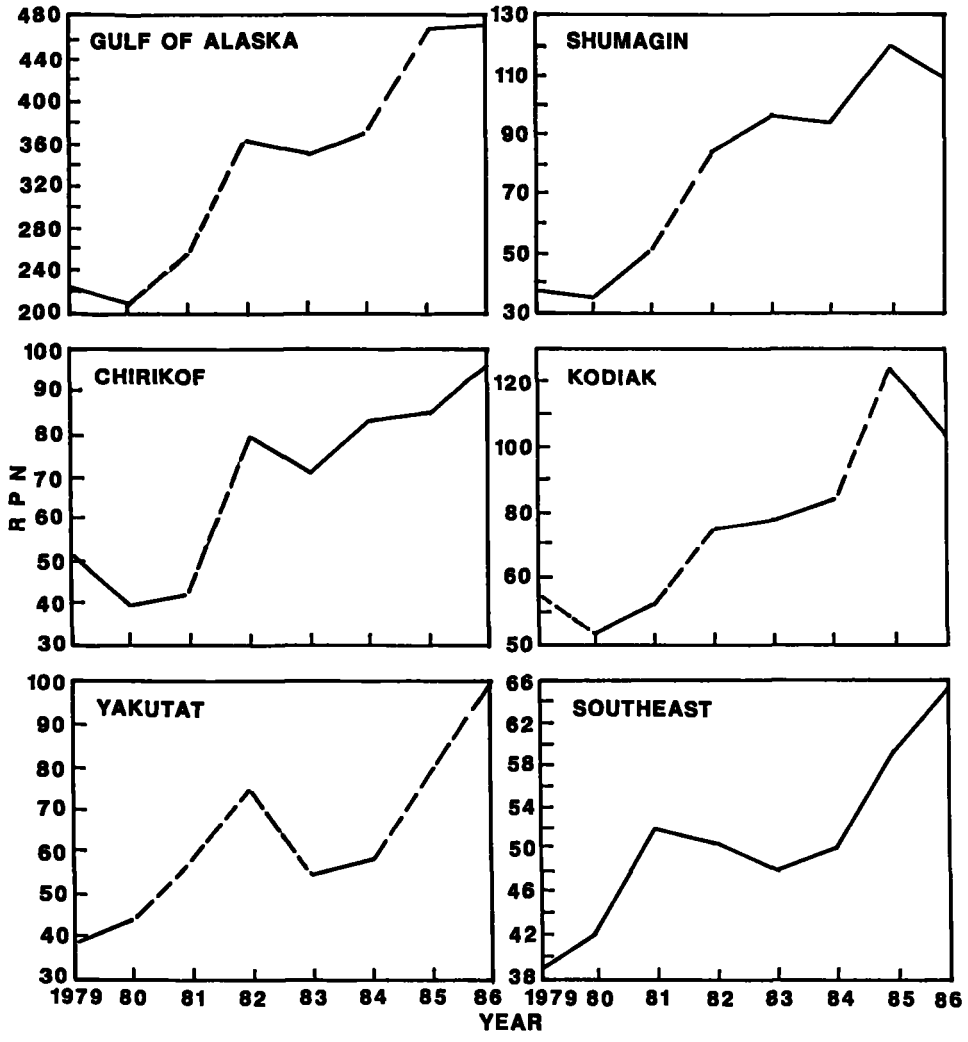

FIGURE 3.—Relative population number (RPN) for the Gulf of Alaska and the Shumagin, Chirikof, Kodiak, Yakutat, and Southeastern areas, 1979–86. Dashed lines (---) signify that the annual change was statistically significant.

to 1982, and 1984 to 1985 (Fig. 3). Differences between other years were not significant.

The RPN for each of the statistical areas of the Gulf of Alaska generally increased from 1979 to 1986 (Fig. 3); the differences between 1979 and 1986 were statistically significant for all areas (Table 3), showing that sablefish abundance has increased throughout the Gulf of Alaska. The sharp jump in the RPN for the Gulf of Alaska from 1980 to 1982 was caused by significant increases in four areas, Shumagin, Chirikof, Kodiak, and Yakutat. The sharp jump from 1984 to 1985 was caused by significant increases in two areas, Kodiak and Yakutat.

DISCUSSION

As noted earlier, sometimes not all strata were sampled at a station (Table 1). This shortcoming was a consequence of the length of the sampling gear and the topography at a station. At stations where the bottom gradient was slight for all or part of the station, the 16 km of longline gear sometimes was not long enough to sample all strata. As a result, sometimes no stations were sampled within certain strata. For these strata, catch per hachi values were estimated using combined data from the current and previous year's data. The resultant values are esti-

TABLE 3.—Statistical significance of annual changes in relative population number of sablefish, Gulf of Alaska, Japan-U.S. cooperative longline survey, 1979–86. The symbols used are defined as follows: + signifies a significant increase in RPN; – signifies a significant decrease in RPN; O signifies no significant change.

Area	Year	80	81	82	83	84	85	86
Gulf of Alaska	1979	O	+	+	+	+	+	+
	1980		+	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	+	+
	1984						+	+
	1985							O
Shumagin	1979	O	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	O	O
	1984						O	O
	1985							O
Chirikof	1979	O	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	O	+
	1983					O	O	+
	1984						O	O
	1985							O
Kodiak	1979	–	O	+	+	+	+	+
	1980		O	+	+	+	+	+
	1981			+	+	+	+	+
	1982				O	O	+	+
	1983					O	+	+
	1984						+	O
	1985							O
Yakutat	1979	O	+	+	+	+	+	+
	1980		+	+	O	+	+	+
	1981			+	O	O	+	+
	1982				–	–	O	+
	1983					O	+	+
	1984						+	+
	1985							+
Southeastern	1979	O	+	+	O	+	+	+
	1980		O	O	O	O	+	+
	1981			O	O	O	O	+
	1982				O	O	O	+
	1983					O	O	+
	1984						O	+
	1985							O

mates of catch per hachi as if the strata had been sampled. Because the estimated values mimic the observed data, the probability of rejecting the null hypothesis is somewhat higher than the nominal value. In general an inaccurate estimate should have a small total effect because catch per hachi values were missing for only 9 of the 320 strata available during the survey (8 years × 5 areas × 9 strata). The only comparison where the estimated catch per hachi values might have caused an incorrect conclusion is the 1984–85 comparison where 7 strata were unsampled. This comparison was retested using only the observed catch per hachi values. The annual change, like the comparison using the estimated catch per hachi values, was found to be statistically significant.

Another potential effect of incomplete sampling at a station is bias in the bootstrap calculation. Each bootstrap replicate $RPN_{i,k}^*$ was computed from a bootstrap sample selected by sampling with replacement from the stations within an area. If one or more stations were missing an observation for a strata, then it was possible for the bootstrap sample to have all missing values for the strata. In this case, no catch per hachi values were available to calculate a value for the strata and the value for the strata was treated as zero. This treatment may negatively bias the resultant $RPN_{i,k}^*$. The extent of the negative bias was tested by comparing the RPN to a bootstrap estimate of the RPN, denoted RPN_b, where RPN_b is the mean of the 1,000 $RPN_{i,k}^*$ from an area and year. If RPN_b generally was smaller than RPN, then the bootstrap replicates were negatively biased. The percentage difference between the resultant RPN_b's compared to the RPN's ranged from −0.7 to +0.5 and averaged only +0.03, showing that the negative bias had little effect on the $RPN_{i,k}^*$.

Other fishery and survey data substantiate the significance of the overall increase in the RPN and also the marked increases from 1981 to 1982 and from 1984 to 1985. The CPUE in the Japanese longline fishery showed a similar pattern to the RPN's for the years the data overlapped, from 1979 to 1983; the fishery CPUE increased from the late 1970's, with the largest increase from 1981 to 1982, and decreased from 1982 to 1983 (Fig. 4).

Examination of length compositions for depths 101–200 m indicate that the strong 1977 year class (Sasaki 1982; McFarlane and Beamish 1983; Funk and Bracken 1984) was responsible for the RPN increase from 1980 to 1982 and that the RPN increase from 1984 to 1985 was due to a strong 1980 year class. Sablefish recruiting to the survey area first appear at depths 101–200 m, and strong year classes are more distinguishable in the length compositions at these depths. The length compositions for depths 101–200 m show the initial appearance and subsequent increase in length of fish of the strong 1977 year class (Fig. 5). The mode at 47 cm FL in 1979 indicates the first year that the 1977 year class was available to the survey gear. The rightward movement of the mode in succeeding years illustrates the increase in fish length for the 1977 year class. The movement of the mode slowed in 1982 which we interpret to be due mainly to the movement of larger

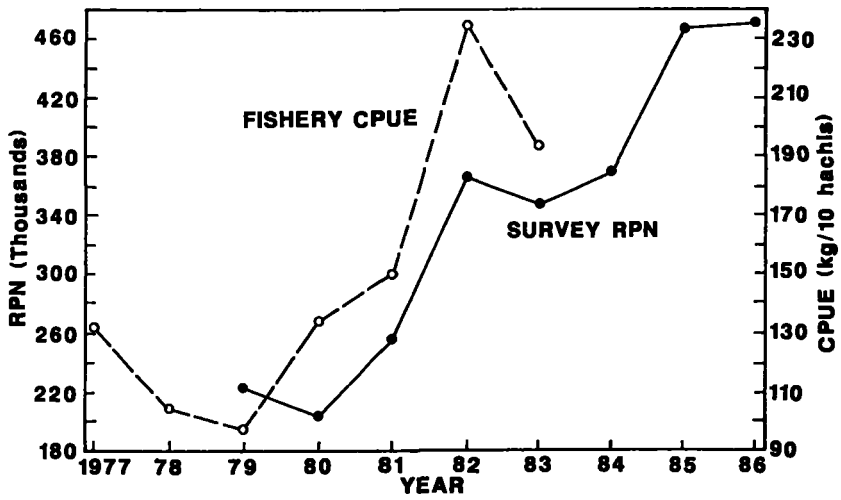

FIGURE 4.—Sablefish catch per hachi (kg/10 hachis) for the Japanese longline fishery, 1977–83 (Fujioka 1986) and relative population number (RPN), 1979–86.

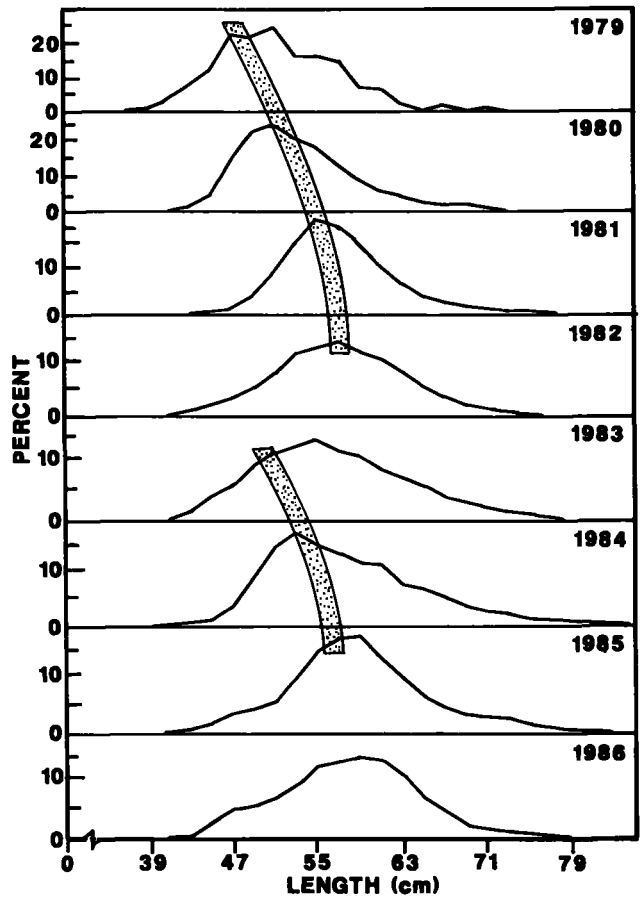

FIGURE 5.—Length-frequency distributions of sablefish in the Gulf of Alaska for depths 101–200 m, 1979–86. The shaded bands illustrate the progression of the modes of two strong year classes, 1977 and 1980.

fish to depths >200 m. The timing of this movement corresponds to the year that the RPN significantly increased.

The pattern of length compositions from 1983 to 1985 parallels those due to the strong 1977 year class and suggests that the 1980 year class is also strong (Fig. 5). The shoulder at 49–51 cm FL in 1983, not present in 1982, indicates the first year that the 1980 year class was available to the survey gear. This shoulder is due to distinct modes at 47–51 cm FL in the Chirikof, Yakutat, and Southeastern areas. The rightward movement of the mode in succeeding years illustrates the increase in fish length for the 1980 year class. The mode at 53 cm FL in 1984 is similar to the modes at 50–57 cm FL found in the Gulf of Alaska for depths 101–200 m during a trawl survey conducted in 1984 by the Northwest and Alaska Fisheries Center (Brown 1986) and is further evidence for a strong 1980 year class. The rightward movement of the mode slowed in 1985, presumably due to movement of larger fish to depths >200 m, and again corresponds to the year of a significant increase in RPN.

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PELAGIC BIOGEOGRAPHY OF THE ARMORHEAD, *PSEUDOPENTACEROS WHEELERI*, AND RECRUITMENT TO ISOLATED SEAMOUNTS IN THE NORTH PACIFIC OCEAN

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ABSTRACT

The pelagic armorhead, *Pseudopentaceros wheeleri*, occurs widely in the North Pacific Ocean. Benthic specimens have been taken from Japan, the Hawaiian Archipelago, and the west coast of North America, but the main reproductive populations are located on southern Emperor-northern Hawaiian Ridge seamounts between lat. 29° and 35°N. The period between spawning and recruitment to the seamounts is apparently between 1.5 and 2.5 years, suggesting an extended pelagic existence. We describe the distributional patterns in the North Pacific based upon over 30 years of published and unpublished records. The majority of pelagic specimens are captured in the subarctic water mass in the northeast Pacific. Based upon the distributional patterns and the oceanography of the North Pacific, we propose migratory paths for both the main population and for the individuals that occur rarely in other locations. The long pelagic period and variability in ocean conditions may play an important role in recruitment to seamounts and the variability in year-class strength for this species.

The pelagic armorhead, *Pseudopentaceros wheeleri*, is a member of the boarfish family Pentacerotidae. Until recently, considerable confusion existed about its taxonomy and distribution. Originally described as *Pentaceros richardsoni* Smith 1844, it was thought to be distributed virtually worldwide, with centers of abundance in the North Pacific and in the South Atlantic near South Africa (Fujii 1986). Occurrences were typically sporadic; most records were from pelagic captures, hence the name pelagic armorhead. Several authors, including Welander et al. (1957), Clemens and Wilby (1961), and Wagner and Bond (1961), used the name *Pseudopentaceros richardsoni*, but more recent studies used the original binomial following Follett and Dempster (1963).

The 1967 discovery of large concentrations of armorhead in the mid-Pacific, over southern Emperor-northern Hawaiian Ridge (SE-NHR) seamounts (from lat. 29° to 35°N) (Sasaki 1974; Uchida and Tagami 1984) stimulated increased interest in this species. Over the next 10 years, nearly 1 million metric tons (t) were taken by Soviet and Japanese trawlers (Borets 1975; Takahashi and Sasaki 1977). The increased availability of specimens allowed Hardy (1983) to revise the family. He first separated the *Pentaceros richardsoni* complex from other members of the genus by referring it to *Pseudopentaceros* Bleeker, based on morphological considerations. Second, he separated the complex into three species: *P. richardsoni* confined to the Southern Hemisphere, and *P. wheeleri* and *P. pectoralis* in the North Pacific. The features used to distinguish *P. wheeleri* and *P. pectoralis* were largely morphological. *Pseudopentaceros pectoralis* is more robust and deeper bodied and its distribution is typically pelagic; *P. wheeleri* was known only from benthic specimens on seamounts. Hardy (1983), however, lacked transitional specimens; subsequent work based on morphological and electrophoretic grounds revealed that *P. wheeleri* was a morphological derivative of *P. pectoralis*, with changes occurring after settlement. The deeper bodied pelagic form ceases growth in length after recruiting to the seamounts and instead transforms body shape to a leaner form. "Fat" and "lean" specimens of the same length thus differ significantly in appearance (Humphreys et al. in press).

Pseudopentaceros wheeleri has an unusual life history. Spawning occurs at the benthic population centers at the SE-NHR seamounts between November and March (Sasaki 1974; Borets 1976; Bilim et al. 1978). Larvae and juveniles are pelagic (Honma and Mizusawa 1969; Fedosova and Komrokov 1975; Borets and Sokolovsky 1978) and widely distributed in the North Pacific. Recruitment to the seamounts

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occurs between ages 1.5 and 2.5 years, but in the major spawning population centers, over 95% of the fish are <2 years (Uchiyama and Sampaga[3]). This lack of older specimens and presence of fish in poor physiological condition has led to suggestions that this species is semelparous, with death after a single spawning (Humphreys and Tagami 1986; Humphreys et al. in press). The long interval between spawning and recruitment for this species suggests that oceanographic conditions in the North Pacific regulate its distribution (Boehlert 1986).

Published records of the pelagic distribution of *P. wheeleri* are too few and varied to understand its biogeography. In different years, specimens have been caught in the Gulf of Alaska, near the Aleutian Islands, and off the coasts of Japan, Oregon, California, and British Columbia. In this paper, we document the pelagic and benthic occurrences from both published and unpublished accounts, consider this distributional pattern in light of general oceanographic conditions in the North Pacific, propose hypotheses about the migration and recruitment of armorhead to the seamounts of the central North Pacific, and assess interannual variation in abundance and how it may relate to oceanographic variability.

[3]Uchiyama, J. H., and J. Sampaga. In review. Age and growth of the pelagic armorhead, *Pseudopentaceros wheeleri*, at Hancock Seamounts. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396.

MATERIALS

The data sources used include published and unpublished collection records from throughout the North Pacific Ocean. Published records on occurrences in Japan (Abe 1957, 1969; Zama et al. 1977; Okamura et al. 1982), the eastern North Pacific (Welander et al. 1957; Larkins 1964; Honma and Mizusawa 1969; Chikuni 1970; Ignell et al. 1986), and the west coast of North America (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965) were typically of single or a few specimens. Larger numbers of unpublished collection records were in data from large-scale surveys (Table 1). These data

TABLE 1.—Data bases searched for pelagic armorhead, *Pseudopentaceros wheeleri*, captures excluding single collections and literature reports. Areas and seasons are averages over the years covered.

Data source	Years, season effective	Area	
		Lat. N	Long.
Salmon drift gill-net surveys[1]	1972–86, spring-fall	38°–65°	140°E–166°W
University of Washington (FRI) purse seining, longlining[2]	1956–82, spring-summer	42°–60°	165°E–125°W
Canada salmon longlining[2]	1962–67, spring-summer	42°–54°	120°–145°W
Bureau of Commercial Fisheries salmon gill net[2,3]	1955–71, spring-summer	40°–60°	165°E–125°W
Oshoro Maru salmon gill-net-longline surveys[4]	1963–66, 1968, 1969, 1971, 1974–86, spring-summer	36°–66°	163°E–124°W
Hokusei Maru squid and salmon gill-net surveys[4]	1973–86, summer	18°–58°	141°E–156°W
Japan Marine Fishery Resource Research Center pomfret surveys[5]	1979–82, all months	22°–49°	143°E–124°W
Japanese commercial whaling reports[6]	1952–79, summer	40°–58°	
Pacific Biological Station gill-net surveys[7]	1983, 1985–86, spring-summer	47°–54°	138°–130°W
Taiwan Fisheries Research Institute squid surveys[8]	1986, July-August	38°–46°	153°E–175°W
National Marine Fisheries Service Auke Bay cooperative squid gill-net surveys[9]	1985–86	43°–55°	145°–175°W
Japan Fisheries Agency squid gill-net surveys	1986–87, July-August	36°–47°	150°–165°W

[1]Salmon research data file, North Pacific Ocean, 1972–86. Salmon Division, Far Seas Fisheries Research Laboratory, Shimizu, Japan.
[2]Macy et al. 1978.
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[6]Biological data file of whales in the North Pacific Ocean, 1952–79. Whale Section, Far Seas Fisheries Research Laboratory, Shimizu, Japan. See also Chikuni (1970).
[7]Sloan 1983; Robinson and Jamieson 1984.
[8]Z. Shyu, Taiwan Fisheries Research Institute, Keelung 20220, Taiwan, pers. commun. May 1987.
[9]Ignell et al. 1986.

are seasonally limited to primarily spring, summer, and early fall months, but cover 1952–87 and provide broad geographic coverage between lat. 18° and 66°N. Greater detail and a summary of many of these surveys are provided by Macy et al. (1978). Since armorhead were an incidental catch, it is difficult to assess the relative value of the different surveys with respect to sampling effort.

The most typical sampling gears used were longlines, gill nets, and purse seines targeting salmon, squid, or pomfret; rarer collections were made with plankton nets, dip nets, or hook and line. Thus, sampling was typically in surface waters, most likely in the upper 50 m; the true depth distribution of the pelagic animals, however, is unknown. The only other "gear" was the sei whale, *Balaenoptera borealis*, from which stomach contents were studied for about 27 years; Chikuni (1970) reported armorhead in the stomachs.

RESULTS AND DISCUSSION

Distributional Patterns

The known center of distribution and spawning for benthic *P. wheeleri* is in the SE-NHR seamount region, bounded by lat. 29°–35°N and long. 171°E–179°W (Takahashi and Sasaki 1977; Humphreys and Tagami 1986). These reproductive fish are typically between 23.0 and 28.5 standard length (SL) (Sasaki 1986) and range in age from 1.5 to 2.5 years (Uchiyama and Sampaga fn. 3). They are found at depths between 200 and 500 m (Takahashi and Sasaki 1977). Other benthic occurrences have been recorded but are sporadic (Fig. 1). Several specimens were captured off Japan in 1957 (Abe 1957), 1969, 1971–73, 1976 (Zama et al. 1977), and 1979 (Okamura et al. 1982). These fish were typically the same size as those captured on the seamounts, but no mention of reproductive status was made. Fish of similar length occur rarely on the west coast of North America, but only between lat. 37°00′ and 44°25′N (Wagner and Bond 1961; Follett and Dempster 1963; Smith 1965). Again, reproductive status is unknown for these specimens. No benthic occurrences off British Columbia or Alaska have been reported, despite extensive trawling surveys which included seamounts (Hughes 1981; Alton 1986). Large specimens have been taken rarely in the Hawaiian Archipelago (Fig. 1; Randall 1980; Humphreys et al. in press) and are typically 4–5 years old and appear to be in reproductive condi-

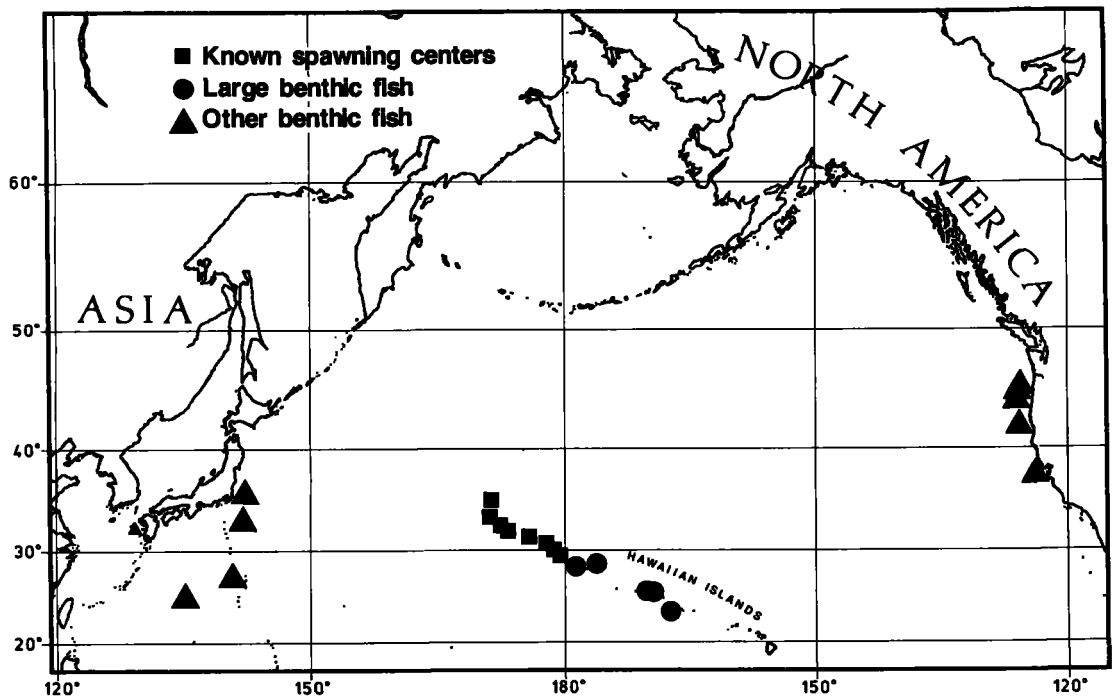

FIGURE 1.—Known distribution of benthic occurrences of pelagic armorhead, *Pseudopentaceros wheeleri*. Squares represent the main population centers at central North Pacific seamounts. All others are rare or sporadic occurrences.

tion. Their relationship with the SE-NHR seamount populations is unknown.

The most common pelagic occurrences (1955–87) were fish ranging from 18 to 26 cm SL; smaller sizes are poorly represented, probably because of the nature of the sampling gear. Smaller specimens were generally captured with plankton nets (Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), dip nets (Honma and Mizusawa 1969; Randall 1980; Fujii[4]), and in one case, in a whale stomach (Kawamura 1982). The sea-surface temperatures at which the specimens were captured ranged from 8.6° to 15.0°C (average 12.1°C). For all years, pelagic captures were restricted to the eastern North Pacific, with the exceptions of larvae or early juveniles captured near the spawning centers at the seamounts (Komrakov 1970; Table 2), over 20 specimens in a Bryde's whale stomach in 1979 (Kato[5], Fig. 2B), and two individuals captured in 1986 at long. 155°E (Fig. 2). This is despite extensive sampling in the western North Pacific, particularly by the Japan Marine Fishery Resource Research Center (JAMARC) and the Hokkaido University, and in the Bering or Okhotsk Seas (Table 1).

Pelagic captures in the 1950's were sporadic, but several fish were taken north of lat. 50°N, especially in 1958 (Fig. 2A). Relatively few were captured in the 1960's, with the exception of July through early August 1969, when the armorhead was an impor-

[4]E. Fujii, Nippon Luther Shingaku Daigaku, Tokyo, Japan, pers. commun. July 1987.

[5]H. Kato, Whales Research Institute, Tokyo, Japan, pers. commun. December 1987.

TABLE 2.—Pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, for which sizes were available. The growth curve from Uchiyama and Sampaga (text footnote 3), based upon enumeration of daily growth increments, was used to deduce age from length. For the youngest fish (bottom), average readings from daily growth increments, rather than the growth curve, were used. Data are from various published sources and collections listed in Table 1. (SST = sea-surface temperature.)

Year	Date	Lat. N	Long.	SST	Standard length (mm)	Age (yr)	No.	Gear
1955	9/27	45°41′	165°5′W	—	108–122	0.38–0.42	2	Gill net
1955	9/27	45°35′	165°5′W	—	200	0.79	1	Dip net
1956	7/31	45°49′	160°3′W	12.2	245	1.29	1	Gill net
1956	9/15	45°00′	155°00′W	12.1	245	1.29	2	Gill net
1956	9/17	49°00′	150°00′W	13.2	245	1.29	1	Gill net
1956	9/17	51°00′	150°00′W	11.0	245	1.29	1	Gill net
1958	8/14	44°39′	174°48′W	—	64–91	0.26–0.33	2	Dip net
1958	8/25	49°43′	146°10′W	11.8	256	1.50	1	Gill net
1963	8/24	49°0′	162°0′W	12.9	249	1.40	1	Gill net
1967	6/15	54°38′	150°1′W	8.8	121–134	0.42–0.46	4	Dip net
1968	7/	41°30′	165°30′W	—	285	>2.00	1	Handline
1969	4/1	29°48′	179°5′E	—	8–23	0.08–0.25	?	Plankton
1969	4/1	31°6′	176°0′E	—	8–23	0.08–0.25	—	Plankton
1969	4/1	32°6′	173°0′E	—	8–23	0.08–0.25	—	Plankton
1972	5/21	38°30′	175°3′W	14.3	42–50	0.21–0.23	5	Whale stomach
1984	7/25	45°30′	155°0′W	13.0	262–265	1.81–2.02	3	Gill net
1984	7/25	45°26′	154°58′W	12.0	278	>2.00	2	Longline
1985	7/9	46°57′	129°4′W	—	272	>2.00	1	Gill net
1985	7/10	47°30′	128°36′W	—	272–298	>2.00	2	Gill net
1985	7/11	47°59′	129°19′W	—	277	>2.00	1	Gill net
1985	7/13	46°23′	131°29′W	—	188–219	0.71–0.94	5	Gill net
1985	7/14	46°40′	131°8′W	—	183–233	0.68–1.1	9	Gill net
1985	7/15	46°35′	131°5′W	—	206	0.83	1	Gill net
1985	7/19	46°54′	131°28′W	—	190–217	0.72–0.92	2	Gill net
1985	7/21	47°18′	130°23′W	—	191–220	0.73–0.95	3	Gill net
1985	7/22	47°35′	130°48′W	—	190–201	0.72–0.79	2	Gill net
1985	7/23	47°37′	130°31′W	—	198–200	0.77–0.79	2	Gill net
1985	7/12	47°0′	155°1′W	11.6	263–265	1.87–2.02	2	Longline
1985	7/13	45°28′	155°5′W	11.8	238–262	1.17–1.81	12	Longline
1985	7/11	47°0′	155°0′W	11.6	248–262	1.35–1.81	5	Gill net
1985	7/12	45°30′	155°0′W	11.8	235–240	1.12–1.20	4	Gill net
1985	7/13	44°0′	155°0′W	12.8	248–258	1.35–1.63	4	Gill net
1985	2/23	30°16′	181°18′W	—	8–15	0.08–0.16	15	Neuston
1985	2/24	29°27′	180°56′W	—	5–15	0.04–0.16	15	Neuston
1986	8/3	43°51′	164°54′W	13.0	50–100	0.23–0.35	5	Dip net

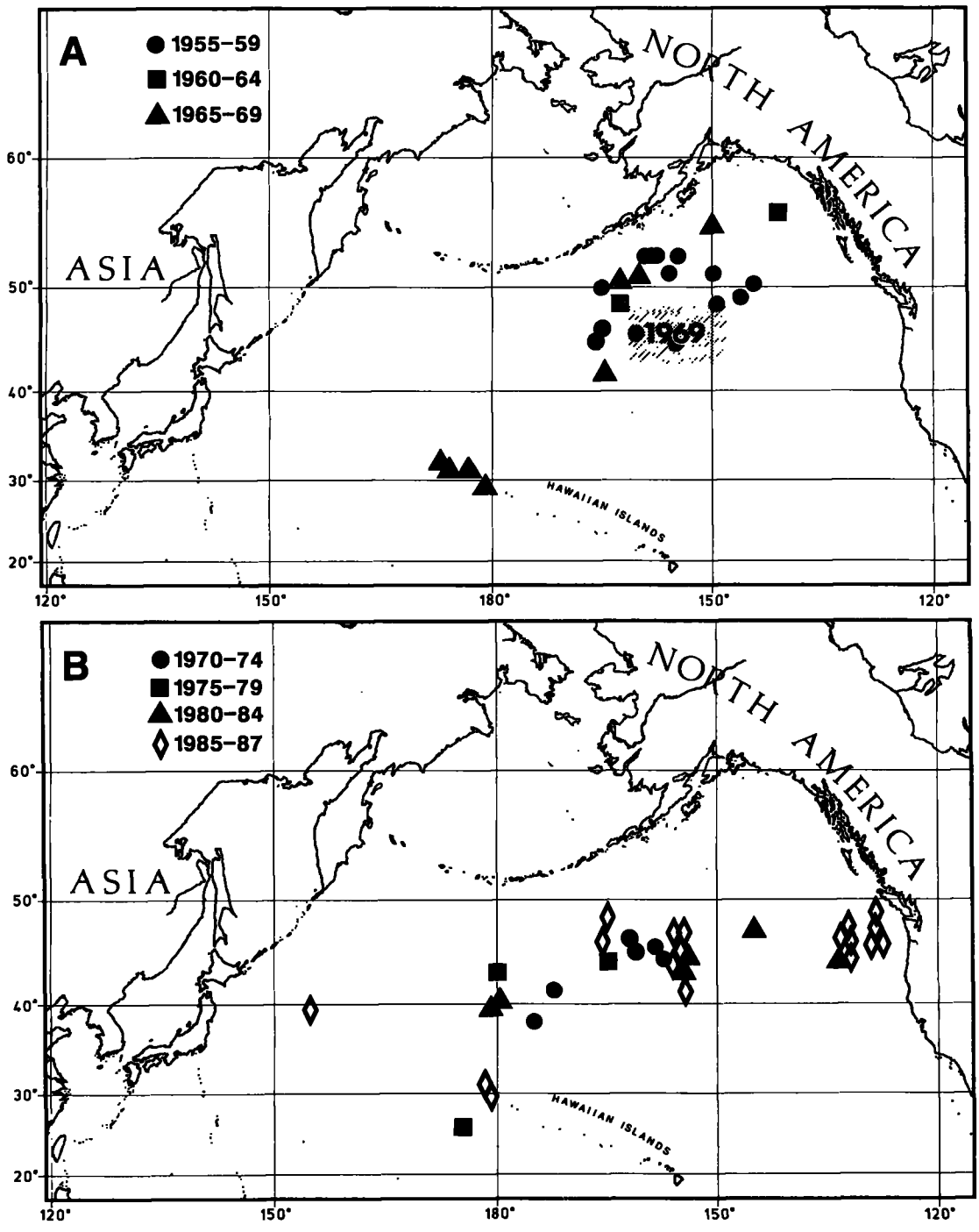

FIGURE 2.—Records of pelagic occurrences of armorhead, *Pseudopentaceros wheeleri*, in the North Pacific. Most data were obtained from either published records or unpublished data described in Table 1: Each symbol represents a collection taking armorhead, rather than single specimens. (A) 1955–69. Here, note that the area in the box contains the locations of 195 sei whales captured in July–August 1969 that had fed extensively upon armorhead. The samples from the central Pacific were larvae and early juveniles (Fedosova and Komrakov 1975). (B) 1970–87.

tant diet component of sei whales taken by the Japanese commercial fleet. This species normally feeds on zooplankton and micronekton (Kawamura 1982), but in this year, 195 whales were recorded to have fed extensively on armorhead. Although data records for whale stomach contents extend from 1952 to 1979, 1969 was the only year when large numbers fed on armorhead, with the exception of two occurrences each in 1971 and 1972. Based on the known feeding mode of sei whales, Chikuni (1970) suggested that the armorhead apparently schools in surface waters. In the 1970's, catches were relatively small, but in the 1980's, specimens have been captured in each year, with the greatest catches in 1985. In that year, fish occurred in more easterly areas as compared to other years.

Relationship of Distribution Patterns to North Pacific Oceanography

The SE-NHR seamounts are located in the mid-Pacific transition zone, between subarctic and subtropical water masses (Roden 1970). The spawning season of armorhead typically lasts from late November through March (Sasaki 1974; Bilim et al. 1978), and larvae are neustonic, at least through the first few months of life (G. W. Boehlert unpubl. data). Near surface drift in this region is largely wind driven (McNally 1981); as shown by Lagrangian drifters, mean surface flow in the SE-NHR seamount region during winter months is typically eastward (Kirwan et al. 1978; Emery et al. 1985) or southeastward (McNally et al. 1983), and long-term mean Ekman transport has a southeastward component (Favorite et al. 1976). Based on mean ship-drift data, progressive vector diagrams over a 3-mo period, with starting points at four SE-NHR seamounts (Bakun[6]), show this typical eastward flow with a southward component (Fig. 3). If pelagic armorhead followed such a pattern, individuals would remain in the subtropical gyre, continuing eastward and then turning south, entering the California Current system. The scarcity of specimens in this region (Figs. 1, 2) suggests instead that most fish move northeastward in some manner, entering subarctic waters and residing within the Alaska gyre; surface drift in winter is northeastward in anomalous years (McNally 1981), and average

[6]Compilation by the NMFS Pacific Fisheries Environmental Group from historic ship drift files assembled by the U.S. Naval Oceanographic Office (A. Bakun, Pacific Fisheries Environmental Group, National Marine Fisheries Service, NOAA, P.O. Box 831, Monterey, CA 93942, pers. commun. April 1987.

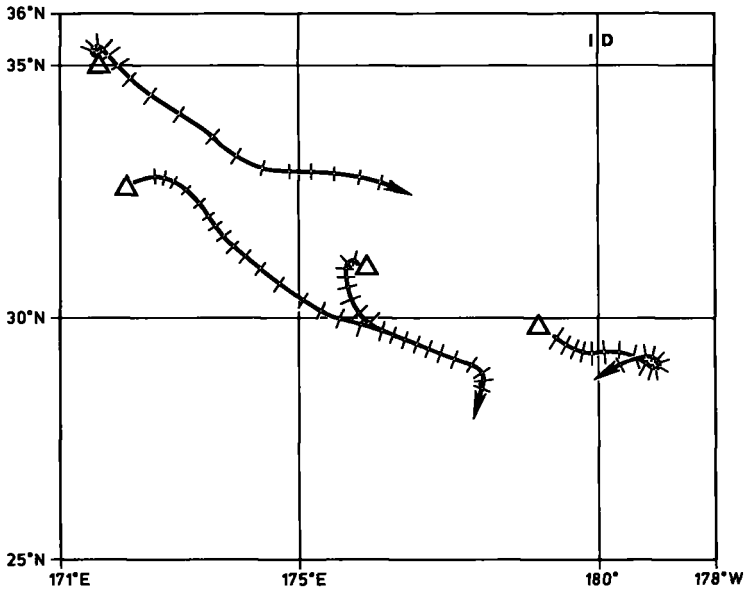

FIGURE 3.—Progressive vector diagrams of mean surface currents (starting date, 15 December; duration, 90 days), from long-term mean ship drift data from 1° squares, with distances calculated on a daily basis. Triangles indicate starting locations at four seamounts with armorhead spawning populations. Each mark on the vector between the origin and arrow represents a 5-d period. See text footnote 6.

surface flow is in this direction in summer months (McNally et al. 1983).

The two available studies on larval distribution of armorhead are conflicting and suggest that patterns of movement may differ from year to year. Komrakov (1970) conducted surveys in March–April 1969 and observed larvae only at northern seamounts and in the open ocean several hundred kilometers northeast of the SE-NHR seamounts. Borets (1979), however, observed 5–20 mm larvae remaining mostly around the seamounts, with highest abundance south of lat. 33°N in 1976. Because spawning occurs at seamounts northwest of this area, this pattern is consistent with southeastward drift during the first few months of life (Fig. 3). If larvae remain in the seamount region, they could be transported to the northeast in summer months, or they may actively migrate northeastward after reaching the juvenile stage. A similar migration apparently occurs for the pomfret, *Brama japonica*, which prior to spawning moves into the North Pacific current region in a broad latitudinal band between the subtropical convergence and the subarctic boundary; immature fish and spent adults then move northward into the subarctic region to feed during April–May (Shimazaki and Nakamura 1981). The pomfret differs from the armorhead, however, in that it remains pelagic throughout its life and also is abundant in the western North Pacific. Larval and juvenile *Brama* sp. do occur in the same area as larval armorhead (Borets and Sokolovsky 1978; G. W. Boehlert unpubl. data).

A possible scenario of movements after the larval stage can be deduced from the ages of individuals captured in different regions. Based upon the growth of pelagic armorhead (Uchiyama and Sampaga fn. 3), most of the larger specimens indicated in Figure 2 are from 1 to 2 years old, and the pelagic duration for this species is most often from 1.5 to 2.5 years. Using daily growth increments for larval and small juveniles and fitted growth curves for larger juveniles and adults, one can convert lengths to ages. The pelagic specimens of known length range in estimated age from 0.04 to >2 years (Table 2). The youngest animals are typically found in the region of the seamounts (Komrakov 1970; Fedosova and Komrakov 1975; Borets and Sokolovsky 1978), but intermediate-sized fish are found north and east of the seamounts. Different age groups seem to be distributed in different areas in the eastern North Pacific (Fig. 4). Armorhead spawn in the seamount region (as area A in Figure 4) during November to March, and juveniles 5–25 mm long are found in the SE-NHR seamounts area from February to early April (Fedosova and Komrakov 1975; Borets 1979). Subsequent occurrences of fish older than 0.25 year (Table 2) are found only in the region northeast of the seamounts and in the Gulf of Alaska (area B in Figure 4). Northeastward movements are contrary to mean ocean currents, but Roden et al. (1982) described intense northward flow along the axis of the southern Emperor Seamounts that could conceivably play a role in transport of fish at the youngest stages.

Recruitment of later stage armorhead to the seamounts requires movement to the west. The only significant westward circulation in the North Pacific is found in the Alaskan Stream (Favorite 1967). This narrow current occurs north of lat. 51°N and extends westerly to near long. 170°E, where it splits to two branches, one turning northerly into the Bering Sea and the other southerly under the influence of the northern Emperor Seamounts or Kormandorskie Ridge (Favorite 1967; dashed line in Figure 4). Darnitsky et al. (1984) described southerly movement of this water to at least lat. 40°N and suggested that it played a role in transport of planktonic food for armorhead on the seamounts. Unless returning armorhead are deep in the water column and therefore not sampled, distributional data (Fig. 2) do not support this route for westerly movement. Fish near recruitment size and age are instead captured in the region marked C on Figure 4, south of the area where younger fish are captured. These fish apparently migrate back to the region of the seamounts by some unknown, but probably active, mechanism.

Two less important, but plausible, movement patterns may explain the rarer occurrences in southern Japan, off Oregon and California, and in the Hawaiian Archipelago (Fig. 4). Chelton (1984) discussed possible interannual changes in the latitudinal position of the West Wind Drift which may lead to differing magnitudes of transport in the Alaska and California Currents. The rare benthic occurrences of the pelagic armorhead off the west coast of North America (area D in Figure 4) may come from specimens that drift southward in the California Current in years of greater southern transport. Some of these may not settle out and remain within the subtropical gyre, possibly recruiting to the Hawaiian chain far to the south of the normal reproductive population. This route, because of its distance, apparently takes considerably longer than that in the subarctic gyre; based upon satellite drifters, McNally et al. (1983) suggested that a full circuit of the subtropical gyre takes 4.5 years. The armorhead collected in the Northwestern Hawaiian

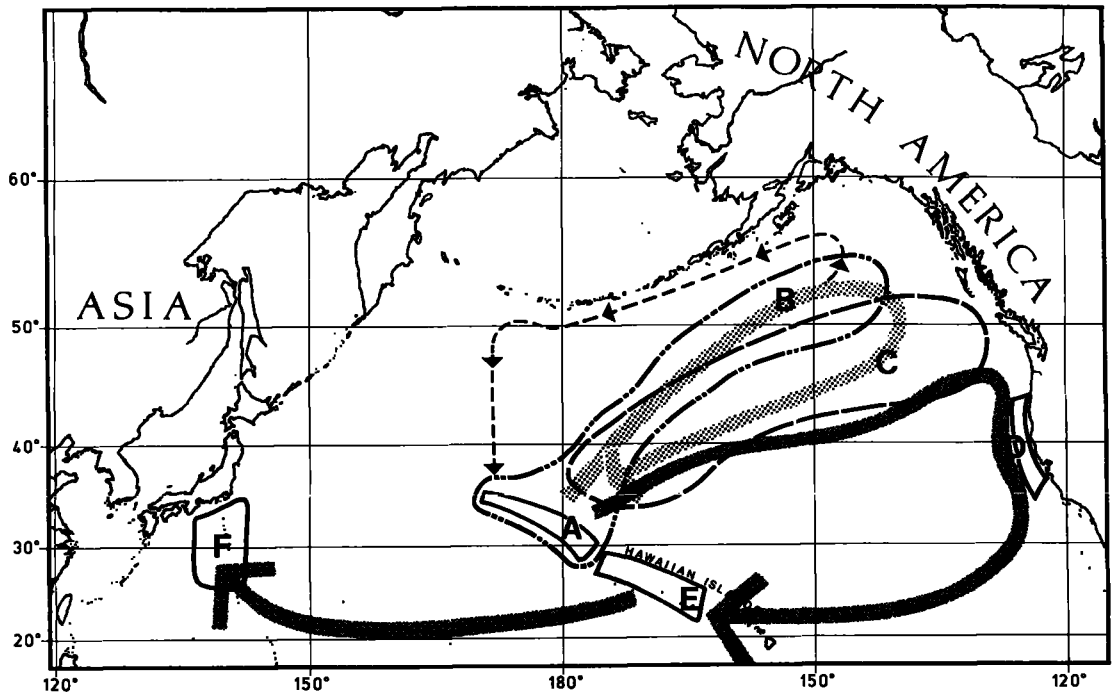

FIGURE 4.—Distributions of benthic and pelagic specimens of armorhead, *Pseudopentaceros wheeleri*, by age group with possible patterns of movement. Area A represents the major spawning area, and area E the region inhabited by the large, older specimens. Area B is the region in which specimens younger than 1 year have been captured, and area C where fish from 1 to 2 years old have been captured. The arrow through this region represents the main population movement pattern. Other arrows represent possible movements for stray fish. Areas marked D and F represent locations of benthic collections from California and Japan, respectively.

Islands (area E in Figure 4) are typically larger than those in the normal part of the range and are correspondingly older, with ages estimated at 4 or 5 years (Humphreys et al. in press), similar to the time suggested for a circuit of the gyre by McNally et al. (1983).

The other plausible movement pattern can be used to explain the existence of specimens in Japan. Benthic specimens of armorhead are rarely captured in Japan (Fig. 1); a report of 3,000 t landed in 1969 by Soviet fishermen in this region (Abe 1969) may be in error, since the Soviet fishery on the SE-NHR seamounts developed heavily that year (Borets 1975) and SE-NHR fish were likely sold in Japan. The reproductive condition of these animals is not known, so the source of the spawning population supplying them is at question. The large, reproductive individuals in area E (Fig. 4) have been found as far south as lat. 23°43'N (Humphreys et al. in press). It is possible that larvae and juveniles are transported to Japan in the northern part of the North Equatorial Current (Uda and Hasunuma 1969). This is consistent with the capture of over 20 fish in a Bryde's whale stomach in September 1979 at lat. 26°N (H. Kato fn. 5; Fig. 2B). Subsequent captures of this species have not been made in Japanese waters, where their presence may require a rare recruitment event from an upstream population source, as has been suggested for seamount populations of lobsters (Lutjeharms and Heydorn 1981). These animals may also remain within a gyral circulation, however, as suggested by the presence of two specimens captured in the Kuroshio in 1986 (Fig. 2B).

Recruitment to the Seamounts

The seasonal timing of the recruitment of the pelagic armorhead to the SE-NHR seamounts is unknown. That no records of larger pelagic fish captured near the seamounts (Fig. 2) exist may be an artifact of sampling in inappropriate seasons or lack of sampling in deeper water. The youngest benthic specimens from the seamounts were slightly in ex-

cess of 1.5 years in early summer (Uchiyama and Sampaga fn. 3) and 2 years in winter, suggesting that some recruitment occurs in spring.

In most fisheries, temporal recruitment patterns can be discerned from length-frequency analyses, because the smaller recruits represent a larger proportion of the population during the season of recruitment. For the armorhead, no increase in smaller size classes is apparent in monthly length-frequency samples. This may be due to cessation of somatic growth after recruitment to the seamount (Humphreys and Tagami 1986; Uchiyama and Sampaga fn. 3). Early recruits, with their deeper bodies and greater fat content, differ morphologically from longer seamount residents. The transition from so-called "fat" to "lean" morphotypes occurs in association with development of gonads (Humphreys et al. in press). Thus, an index of morphological change can be used to detect recruitment patterns, much the same as length frequencies can be used for other species. Condition factor is frequently used to assess "fatness" of fish; it is normally expressed as weight divided by length to a power (typically 3) multiplied by some scaling factor (Ricker 1975). For armorhead, there is a marked change in condition factor with morphological change; newly recruiting fish have high condition factors relative to intermediate or lean fish. By considering the monthly proportion of fish above an arbitrary value of condition factor, we can estimate the influx of new recruits to the seamounts. During May 1972–December 1973, the major influx of new recruits with a high condition factor occurred in April–May 1973 (Fig. 5). The data for 1972 are incomplete, but some recruitment apparently occurred in August and September (Fig. 5). Differences in seasonality of recruitment between 1972 and 1973 may be indicative of interannual variability in temporal recruitment patterns.

An influx of fish to the seamounts may also be reflected in the catch per unit effort (CPUE), an index of stock abundance. Monthly averages of CPUE (in metric tons per hour) by Japanese trawlers for armorhead at the SE-NHR seamounts were highest in March and April (Sasaki 1986). Overall armorhead CPUE decreased continuously from 54.1 t/h in 1972 to only 0.3 t/h in 1982 (Sasaki 1986) and further decreased to 0.06–0.07 t/h in 1983–85 (T. Sasaki unpubl. data). The estimated CPUE in 1986, however, was 0.31 t/h, an increase of four or five times that in the previous year. The CPUE of trawlers operating in May–September 1986 was highest in May, decreased in June and July, but increased slightly in August and Septem-

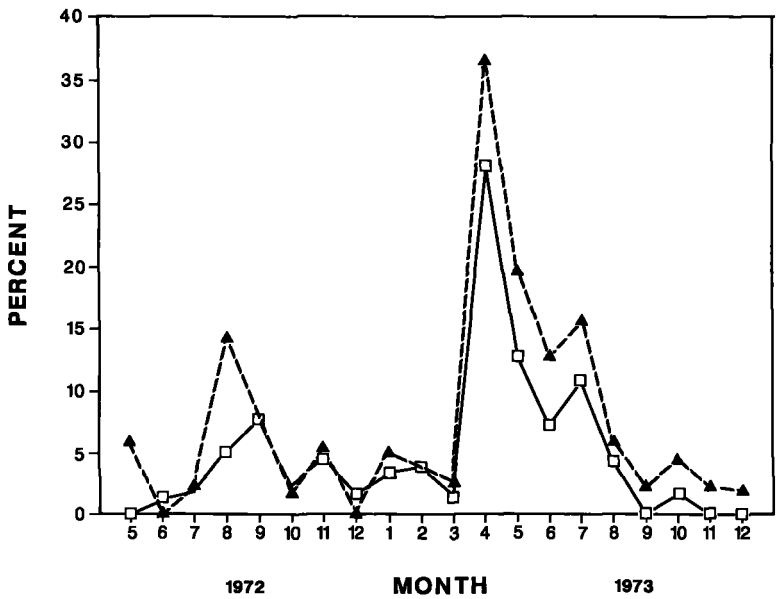

FIGURE 5.—Seasonality of the proportion of armorhead, *Pseudopentaceros wheeleri*, with condition factors ≥2.0 from four seamounts of the northern Hawaiian Ridge (Southeast Hancock, Northwest Hancock, C-H, and Colahan) for 1972–73. Squares, males; triangles, females. Data are based upon 2,104 males and 1,704 females.

ber. Based on all the information, the major recruitment may occur in spring with some additional recruitment in August and September (Fig. 5); data are not sufficient to determine the recruitment pattern in detail.

A broad geographic separation exists between the location of pelagic captures of larger armorhead and the location of the spawning populations (Figs. 2, 4). If recruitment to the seamounts occurs predominantly in spring (as suggested for 1973 in Figure 5), then temporal sampling patterns may have missed these fish, although JAMARC pomfret surveys covered this area in some seasons (Table 1). Locating the seamounts, which have small (2–5 km) summits must be a formidable task given the wide ocean areas over which armorhead are distributed. A similar situation exists for rock lobster, *Jasus tristani*, in the South Atlantic, that recruits from an upstream population some 2,000 km away and in sufficient numbers to support a fishery on Vema Seamount in some years (Lutjeharms and Heydorn 1981).

Open-ocean migrations of fishes may depend upon many potential cues, including electric fields (McCleave and Power 1978), magnetic fields (Walker 1984), gyres (Williams 1972), and pheromones (Nordeng 1977). Certain characteristics of these isolated, open-ocean seamounts may promote their detection by armorhead. First, current-topography interactions may create significant signals in physical and biological features. The region of the SE-NHR seamounts is active in front development (Roden and Paskausky 1978); upwelling, eddies, and other aspects of flow complexity also occur around these seamounts (Roden et al. 1982) and downstream from them (Royer 1978). The biological signals may include increased chlorophyll in response to upwelling or doming of isotherms (Genin and Boehlert 1985), or aggregations of various organisms and the larger animals which prey upon them around seamounts (see review in Boehlert and Genin 1987). Gravity anomalies associated with seamounts may also play a role; positive gravity anomalies exist at the summit and slopes, and negative anomalies are seen in the surrounding "moat" regions (Wedgeworth and Kellogg 1987). Seamounts often have strong magnetic dipoles associated with them, and the dipole might serve as a landmark for magnetic orientation by fish (Klimley[7]). While fish have been shown to have magnetoreceptors (Walker et al. 1985), their use of magnetic maps remains speculative but possible (Gould 1985). Although we cannot postulate the mechanism that armorhead use for recruitment, it is clear that the effects of seamounts may be detected at distances greater than their area alone would suggest.

Interannual Variations in Recruitment Strength

The year-class strength of armorhead recruiting to seamounts appears to be independent of the parent stock size (Wetherall and Yong 1986). As an example, Borets (1975) estimated that on the SE-NHR seamounts from 1968 to 1973, the stock size varied by a factor of <1.8 while recruitment varied by >5.5 times. The relative abundance of armorhead at the SE-NHR seamounts area increased in 1986 after a long period at a very low level. This increase probably corresponds to the high abundance of pelagic specimens captured in the northeastern Pacific in 1985 (Fig. 2B; Table 2) that consisted of two age groups. The increased recruitment at the SE-NHR seamounts in 1986 suggests that environmental conditions were favorable to the survival of young armorhead in the 1984 and 1985 winter seasons.

A wide variety of factors, both biotic and physical, can affect survival and ultimate year-class strength in fishes (Lasker 1978). During the 2 years between spawning and recruitment for armorhead, an extended migration through varied pelagic environments occurs (Fig. 4). Feeding conditions for larval and juvenile stages are characterized by interannual variability; Fedosova (1980) suggested that warm years were more productive for zooplankton prey and, thus, favorable to the survival of young armorhead. Interannual variation in atmospheric systems (Seckel 1988) or large-scale ocean currents of the kind described by Mysak et al. (1982) may also play a role in armorhead recruitment strength. Changes in the position of the Alaska gyre by up to 700 km southwest of its normal position may have occurred from 1981 to 1985, with an associated increase in seawater temperature (Royer and Emery 1987). Large-scale atmospheric phenomena, such as the longitudinal position of the Aleutian Low, may create definite interannual variations in winter wind systems that may be seen in surface current patterns (Seckel 1988). These patterns may, in turn, be related to the latitudinal position of the subtropical front, which varies interannually between lat. 28° and 32°N (Roden 1970). Variability in these features influences surface drift (McNally 1981), which in turn affects the neustonic young of armor-

[7]P. Klimley, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. 30 June 1987.

head. If flow in certain years results in transport of armorhead to other regions (such as the western Pacific or the southern part of the northeast Pacific; Fig. 4), it is possible that large-scale mortalities of armorhead occur later in life, resulting in weak year classes at the SE-NHR seamounts.

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THE TIMING AND SIGNIFICANCE OF DENSITY-DEPENDENT AND DENSITY-INDEPENDENT MORTALITY OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*

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ABSTRACT

We used stock-recruitment, pre- and postrecruitment mortality data for American shad, *Alosa sapidissima*, in the Connecticut River to estimate density-dependent and density-independent mortality rates at the prejuvenile (age 1–100 days) and postjuvenile (age 101 days to 5 years) phases. Total postjuvenile mortality rates from 1967 through 1982 were dominated by density-independent mortality, with only 6% ($Z_{D\,post}$ = 0.30) of the mean total (Z = 4.85) being ascribed to density-dependent processes. By contrast, 23% ($Z_{D\,pre}$ = 1.13) of the total prejuvenile mortality was compensatory, of which nearly all took place during the embryonic and early larval periods. Egg and early larval mortality rates from 1979 through 1987 were positively correlated to June river flows, and inversely related to mean June temperature, whereas mortality rates of all other life stages showed no such relationships. Daily egg and early larval mortality rates from 1979 through 1987 were usually higher and more variable than mortality rates during later stages. There were significant negative correlations between egg and early larval mortality rates and the strength of 1979–87 year classes in the adult stock, whereas mortality rates of late larvae and juveniles were independent of year-class strength. Density-dependent mortality during the egg and early larval stages comprised over 40% of the total mortality at those stages, resulting in the number of midlarvae and juveniles being positively correlated to adult recruitment. These data suggest that year-class strength of American shad in the Connecticut River is established after the egg and larval stages.

It is generally accepted that year-class strength of most fishes is established prior to the juvenile stage from density-independent (climatic factors) and density-dependent (competition, predation, cannibalism) processes (Cushing 1974; May 1974; Goodyear 1980). Although density-dependent mortality is believed to be the mechanism that keeps fish populations stable under low to moderate exploitation (McFadden 1977; Cushing 1980), density-dependent processes such as inter- and intraspecific competition, predation, and cannibalism are difficult to measure. This is particularly so for many highly fecund fishes, whose population sizes undergo wide fluctuations that often cannot be predicted by conventional stock-recruitment models (Parrish and MacCall 1978; Bakun 1984). Despite the acknowledged importance of density-dependent mortality to stock-recruitment theory (Ricker 1975; Ware 1980), few studies have been able to quantify density-dependent mortality, or determine the life stages at which compensation occurs.

Density-dependent mortality may be confined to the prejuvenile stage (Cushing 1974, 1980) or the postjuvenile oceanic stage (Peterman 1978, 1982), or may occur throughout the prerecruitment period (Gulland 1965). The testing of these hypotheses has proceeded slowly because of environmental noise surrounding many stock-recruitment relationships, measurement errors associated with recruitment estimates (Ludwig and Walters 1981), and the lack of long-term mortality data on eggs and larvae.

One species, for which accurate and long-term stock-recruitment and prerecruitment mortality data exist, is the American shad, *Alosa sapidissima*, an anadromous clupeid that spawns in many Atlantic coast rivers (Walburg and Nichols 1967). Previous studies on American shad in the Connecticut River have demonstrated that larval and juvenile mortality rates decline with age (Crecco et al. 1983, 1986) and that growth and survival rates among discrete larval cohorts are significantly affected by short-term hydrographic and meteorological events (Crecco and Savoy 1985b, 1987a). Although previous stock-recruitment studies of Connecticut River shad (Leggett 1977; Lorda and Crecco 1987) found evidence of density-dependent mortality before the juvenile stage, no studies have attempted to estimate density-dependent mortality during the egg and larval stages, or quantify density-dependent and

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density-independent mortality after the juvenile stage.

In this study we used stock-recruitment, pre- and postrecruitment mortality data for American shad in the Connecticut River from 1967 through 1987 to 1) estimate egg mortality rates for the 1979–87 year classes; 2) measure the contribution of density-dependent and density-independent mortality before and after the juvenile stage; and 3) determine the life stage(s) at which most of the density-dependent mortality takes place.

METHODS

Data Source

Estimates of adult recruitment and parent stock size (± SE) from 1967 to 1982 (Table 1) were based on annual population estimates derived by earlier mark-recapture studies (Leggett 1976; Crecco and Savoy 1987[2]) and by the annual mean number of American shad lifted over the Holyoke Dam (Crecco and Savoy 1985a). The parent stock size (PAR_t) from 1967 through 1987 was the annual population estimate of female shad minus that year's commercial catch of female shad. Parent stock (PAR_t) was separated into the parent stock that spawned above the Holyoke Dam (P_a) (Moffitt et al. 1982; O'Leary and Booke 1986[3], 1987[4]) and the spawning stock that spawned below the dam ($P_b = PAR_t - P_a$).

Since female American shad mature between ages four and six, female shad recruitment from the 1967–82 year classes was the sum of virgin 4-, 5-, and 6-yr-old female shad in the 1970–87 runs based on the age-class structure from previous studies (Jones et al. 1976; Leggett 1976; Crecco et al. 1984[5]). Since the sex ratio of mature progeny from each year class is close to 1:1 (Leggett 1976), total recruitment (R_t) from the 1967–82 year classes was estimated by doubling the female shad recruitment estimates. Direct estimates of male shad recruitment are biased by gill net selectivity and differential culling practices of commercial fishermen (Crecco et al. 1984[6]).

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[3]O'Leary, J., and H. E. Booke. 1986. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit Proj. Performance Rep., F-45-R-2, 37 p.

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[5]Crecco, V. A., T. Savoy, and L. Gunn. 1984. Population dynamics studies of American shad in the Connecticut River. CT Dep. Environ. Prot. Final Rep. AFC 13, 76 p.

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TABLE 1.—Estimates of total female American shad parent stock, female spawning stock above and below the Holyoke Dam, mean June flows from 1967 to 1987, and total number of adult recruits from the 1967–82 year classes. SE = standard errors about the estimates × 10^3.

Year	Total spawning stock × 10^3	SE	Spawning stock above × 10^3	SE	Spawning stock below × 10^3	SE	Recruitment × 10^3	SE	June flow m^3/s
1967	167	35	4	0.8	163	34	444	112	437
1968	202	38	5	0.9	197	37	236	59	603
1969	384	70	10	1.8	374	68	490	116	375
1970	413	95	12	2.8	401	92	550	126	243
1971	424	111	14	3.7	410	107	982	205	203
1972	167	40	8	1.9	159	38	430	87	616
1973	111	30	3	0.8	108	29	308	70	534
1974	306	62	10	2.0	296	60	652	139	334
1975	247	65	16	4.2	231	61	560	101	379
1976	435	80	166	31.0	269	49	650	105	286
1977	207	39	112	21.0	95	18	1,240	191	250
1978	210	54	45	12.0	165	42	711	110	488
1979	248	51	87	18.0	161	33	882	127	445
1980	341	58	196	33.0	145	25	1,256	196	201
1981	293	50	143	24.0	150	26	758	132	316
1982	501	67	109	15.0	392	52	282	49	643
1983	423	77	185	34.0	238	43			386
1984	610	67	245	27.0	365	40			661
1985	555	96	219	38.0	336	58			311
1986	392	71	175	32.0	217	39			439
1987	235	37	136	14.0	146	23			250

American shad larvae (10–30 mm TL) were sampled during daylight hours in the Connecticut River with a 6.1 m plankton bag seine (2.4 m deep, wing and bag mesh of 0.505 mm) and 30 m lead ropes from 15 May to 20 July 1979–84, 1986, and 1987. No larval sampling was conducted in 1985. One seine haul was taken weekly at 8–12 fixed stations located throughout the major spawning areas (Fig. 1). Further details on sampling and methods of estimating larval abundance from net samples are contained in Crecco et al. (1983).

Juvenile American shad (40–90 mm TL) were collected weekly from 20 July through 15 October 1967–87 at 7–14 fixed stations located above and below the Holyoke Dam (Fig. 1) based on weekly and biweekly seine surveys (Scherer 1974; Foote 1976; Marcy 1976; Crecco and Savoy 1984). The annual juvenile index of relative abundance (IND_t) from 1967 to 1987 was the mean juvenile catch per seine haul (± SE) from all stations and collection dates (Table 2).

The Timing of Density-Dependent Mortality

Analysis

One of the primary objectives of this study was to determine the magnitude and timing of density-dependent mortality for American shad. Peterman (1978, 1982) found that density-dependent mortality for some stocks of the anadromous sockeye salmon, *Oncorhynchus nerka*, was confined mainly to the 4–5 yr oceanic postjuvenile phase. Given that the Ameri-

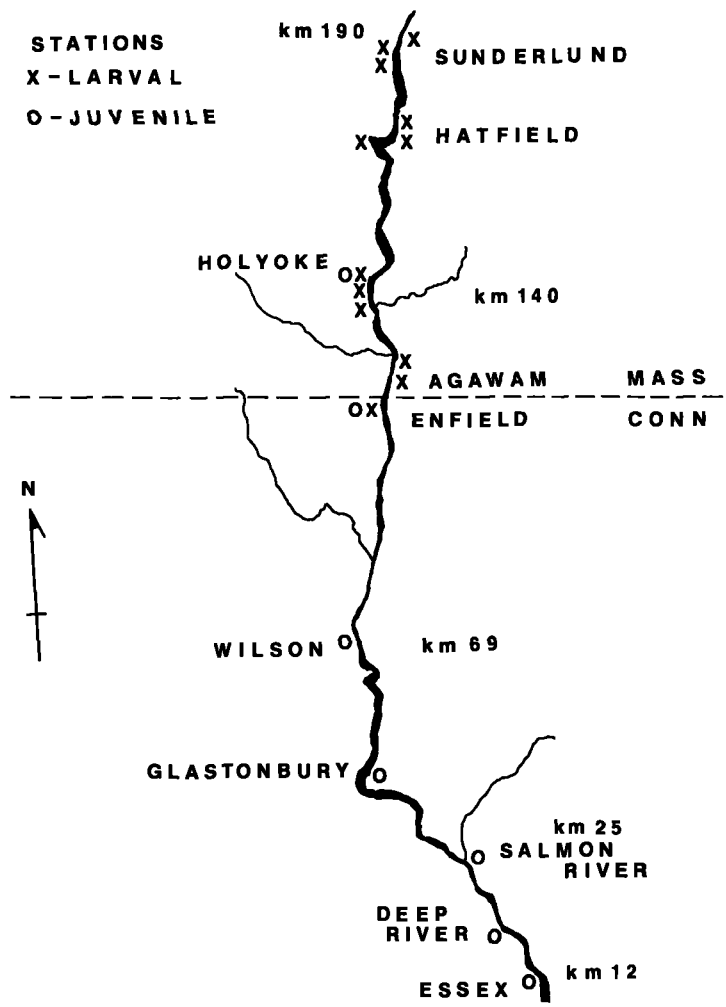

FIGURE 1.—Location of larval and juvenile American shad sampling stations on the Connecticut River.

TABLE 2.—Mean juvenile indices, scaled juvenile abundance from Equation (2) and total egg production for American shad in the Connecticut River from 1967 through 1987. SE = standard errors about the estimates.

Year	Juvenile index	SE	Juvenile abundance $\times 10^3$	SE $\times 10^3$	Total egg production $\times 10^6$	SE $\times 10^6$
1967	20.2	9.4	71,070	33,072	334	70
1968	11.1	1.7	39,053	5,981	404	76
1969	19.0	3.8	68,848	13,770	768	140
1970	27.8	8.2	97,809	28,850	826	190
1971	65.7	14.1	231,151	49,608	848	222
1972	15.3	2.9	53,830	10,203	334	80
1973	12.7	3.4	44,682	11,962	222	60
1974	21.4	6.3	75,292	22,165	612	124
1975	23.7	5.7	83,384	20,054	494	130
1976	22.4	5.9	78,810	20,760	870	160
1977	- - NOT AVAILABLE - -				414	78
1978	27.2	5.9	95,698	20,758	420	108
1979	19.6	3.2	68,959	11,259	496	102
1980	42.7	11.0	150,231	38,701	682	116
1981	16.0	2.7	56,293	9,499	586	100
1982	4.7	1.1	16,536	3,870	1,002	134
1983	26.3	6.6	92,531	23,221	846	154
1984	13.0	2.1	45,738	7,388	1,220	134
1985	17.8	2.7	62,626	9,499	1,110	192
1986	17.0	2.8	59,811	9,851	784	142
1987	44.7	15.1	157,268	53,126	470	74

can shad has a similar 4–6 yr postjuvenile phase as sockeye salmon, we tested Peterman's hypothesis for American shad with key factor analysis (Bellows 1981; Rosenberg and Doyle 1986). We fixed the postjuvenile period for American shad in the Connecticut River between 101 days and 5 years, corresponding to the average age (101 days) at which juvenile shad leave the river (Crecco and Savoy 1985b) and the average age (5 years) when they return to the river as mature adults. The total postjuvenile (age 101 days to 5 years) mortality rates (ZA_t) for the 1967–82 year classes were related to the scaled juvenile indices (J_t) for those year classes (Table 2) in a linear model:

$$ZA_t = a + b(J_t), \quad (1)$$

where $ZA_t = -\log_e(R_t/J_t)$. If significant density-dependent mortality is present during the postjuvenile stage, the slope (b) of Equation (1) would be positive and differ significantly ($P < 0.05$) from

The juvenile indices were scaled to thousands of fish (J_t) so that the y-axis intercept in Equation (1) directly estimates the mean density-independent mortality ($Z_{I\,\mathrm{post}}$), and the slope (b) times the geometric mean juvenile abundance (GM) from 1967 through 1987 is the mean density-dependent mortality rate ($Z_{D\,\mathrm{post}}$). Total juvenile abundance (J_t) was estimated by multiplying the juvenile indices (IND_t) by a scalar (SC):

$$SC = [GR \exp(-EZA) \cdot GM] = 3{,}518.3, \quad (2)$$

where GR is the geometric mean total adult recruitment for 1967 through 1982; GM is the geometric mean juvenile index from 1967 through 1987; EZA (4.85) is the mean total instantaneous mortality among postjuveniles from 1967 through 1982. We estimated EZA as the sum of mortality during the late juvenile period (age 101–365 days), and the subadult stage (age 1–5 years). The mean total instantaneous mortality rate during the late juvenile stage was estimated as 2.65 (0.01 · 265 days), using a mean daily mortality rate of 0.01 (SE = 0.002) extrapolated from the 1979–84 larval and juvenile survivorship curves (Crecco and Savoy 1985b). The mean total instantaneous mortality rate of subadult shad was 2.2, based on an annual instantaneous natural mortality rate of 0.45 from the method of Pauly (1980) plus 0.10 to reflect oceanic fishing mortality (2.2 = 4(0.45 + 0.10)). We estimated the annual natural mortality rate (0.45) by substituting the K (0.25, SE = 0.03) and L (55 cm FL, SE = 3 cm) parameters of the von Bertalanffy equation for male and female shad combined and preferred ocean temperature (14°C) of American shad (Leggett and Whitney 1972) into Pauly's multiple regression model. The oceanic fishing mortality estimate (0.10) was based on tagging studies in Delaware Bay (White et al. 1969; Zarbock 1969) and off the New York-New Jersey coast (Nichols 1958).

To determine if density-dependent mortality takes place during the egg and larval stages as Cushing (1980) hypothesized, we related total prejuvenile mortality rates (ZEJ_t) to annual egg production (Eggs_t), and to both egg production (Table 2) and mean June river flow (JFLOW) from 1967 to 1987 (Table 1) in linear regression models:

$$ZEJ_t = a + b(\mathrm{Eggs}_t) \quad (3a)$$

and

$$ZEJ_t = a + b(\mathrm{Eggs}_t) + c(\mathrm{JFLOW}_t), \quad (3b)$$

where $ZEJ_t = -\log_e(J_t/\mathrm{Eggs}_t)$. Mean June river flows (m^3/s) were included in Equation (3b) because previous studies (Crecco and Savoy 1985b, 1987a) have shown that high June flows reduced prejuvenile survival rates, leading to a significant inverse correlation ($r = -0.74$, $P < 0.01$) between the juvenile indices of abundance from 1967 through 1980 and

mean June river flow (Crecco and Savoy 1984, 1985b). Mean June flows (m^3/s) were measured within the major spawning areas (Leggett 1977) by the United States Geological Survey (U.S. Geological Survey 1967–84). We estimated total egg production ($Eggs_t$) in Equations (3a) and (3b) as the product of the mean fecundity of a female American shad times that year's parent stock (PAR_t) of female shad (Table 1). The average fecundity was reduced from 269,000 ova (Leggett 1969) to 200,000 to reflect the average rates of egg retention and incomplete fertilization (Watson 1970; Reed and Russo 1976[7]). Since Leggett (1969) showed that the average fecundity of American shad varied by less than 10% from 1966 through 1973, we were justified in using an average fecundity for all years.

The mean density-independent mortality rate ($Z_{I\,\mathrm{pre}}$) present during the prejuvenile stage was the y-axis intercept (a) in Equation (3b) plus the slope (c) times the overall geometric mean June flow ($GJFLOW$) from 1967 through 1987:

$$Z_{I\,\mathrm{pre}} = a + c(GJFLOW), \tag{4}$$

The mean density-dependent mortality rate ($Z_{D\,\mathrm{pre}}$) was the slope (b) of Equations (3a) and (3b) times the geometric mean egg production ($G\mathrm{Egg}$) from 1967 through 1987. A positive and statistically significant slope (b) of prejuvenile mortality on egg abundance would support the Cushing hypothesis that density-dependent mortality takes place before the juvenile stage. If the b estimates of Equations (1), (3a), and (3b) were all positive and significant, our results would support Gulland's (1965) hypothesis that density-dependent mortality occurs over the entire prerecruitment phase.

Results

Although total juvenile abundance varied 14-fold from 1967 through 1982 (Table 2), the total postjuvenile mortality rates (ZA_t) exhibited relatively low variability (95% C.I.: 4.70–5.00) about the estimated mean ($EZA = 4.85$) (Fig. 2). The slope of the linear regression between total postjuvenile mortal-

[7]Reed, R. J., and A. Russo. 1976. American shad research Connecticut River, Massachusetts, 1976. I. Fecundity, egg retention, sex ratio, and age class composition. Unpubl. manuscr., 16 p. Massachusetts Cooperative Fisheries Research Unit, University of Massachusetts, Amherst, MA 01003.

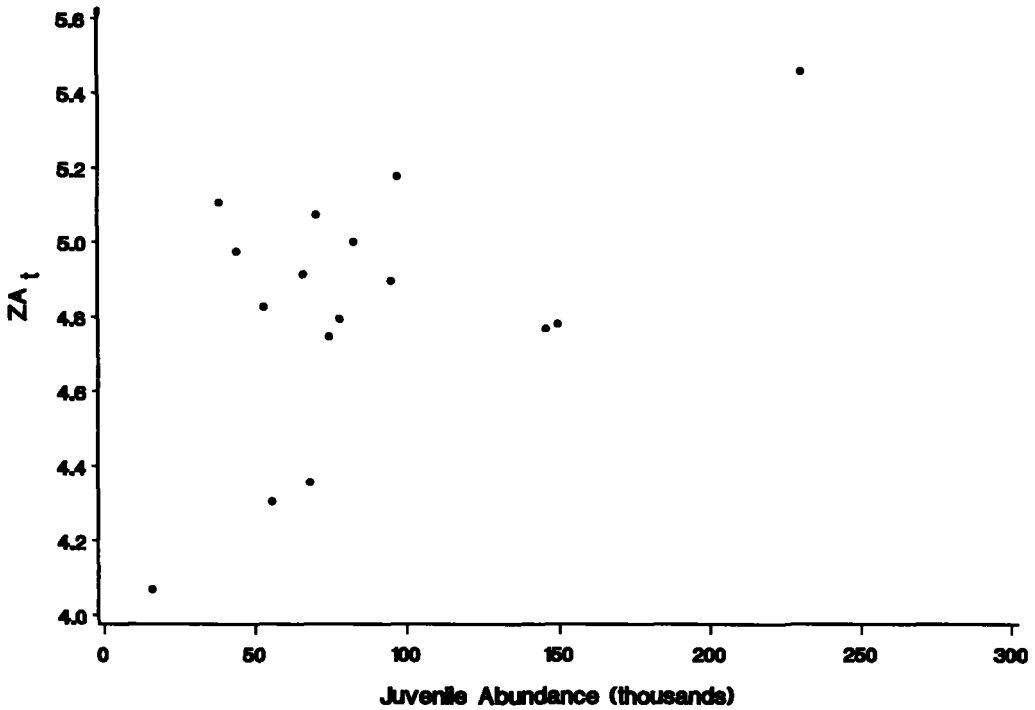

FIGURE 2.—Relationship between American shad postjuvenile mortality (ZA_t) and relative abundance of juveniles (J_t) from 1967 through 1982.

ity rates (ZA_t) and scaled juvenile abundance (J_t) was positive and statistically significant ($P < 0.04$) (Table 3). Since the average density-dependent mortality ($Z_{D\,post} = 0.30$) present during the post-juvenile stage comprised only 6% of the mean total postjuvenile mortality rate ($ZA = 4.85$), density-dependent mortality is not large enough to alter the significant linear correlation ($r = 0.78$, $P < 0.01$) between the juvenile indices (J_t) and adult recruitment (R_t) for the 1967 through 1982 year classes (Fig. 3).

The prejuvenile mortality rates (ZEJ_t) from 1967 through 1987 were positively correlated ($r = 0.70$, $P < 0.0004$) to total egg production ($Eggs_t$) (Fig. 4). Egg production alone explained 49% of the variation in prejuvenile mortality (Table 3) and the slope

TABLE 3.—Estimates of density-dependent (Z_D), density-independent mortality (Z_I) and the fraction of density-dependence ($Z_D/Z_{I+}Z_D$) during the postjuvenile (1967–82) and prejuvenile (1967–87) mortality phases for American shad in the Connecticut River. SE = standard error, and numbers in parentheses = 95% C.I. for Z_D, ZEJ_t = prejuvenile mortality, ZA_t = postjuvenile mortality.

Model	Parameters	SE	Z_D	Z_I	$Z_D/(Z_{I+}Z_D)$
Prejuvenile					
$ZEJ_t = a + b(Eggs_t)$	$a = 5.466$	0.313	1.13	5.47	0.17
	$b = 1.88 \times 10^{-8}$	4.43×10^{-9}	(0.862–1.392)		(0.136–0.203)
	$r^2 = 0.49$				
$ZEJ_t = a + b(Eggs_t) + c(JFlow_t)$	$a = 4.287$	0.303	1.18	5.34	0.18
	$b = 1.97 \times 10^{-8}$	2.87×10^{-9}	(1.007–1.351)		(0.158–0.202)
	$c = 0.0028$	0.0005			
	$r^2 = 0.80$				
Postjuvenile					
$ZA_t = a + b(J_t)$	$a = 4.53$	0.15	0.30	4.53	0.062
	$b = 3.49 \times 10^{-6}$	1.51×10^{-6}	(0.035–0.560)		(0.008–0.110)
	$r^2 = 0.275$				

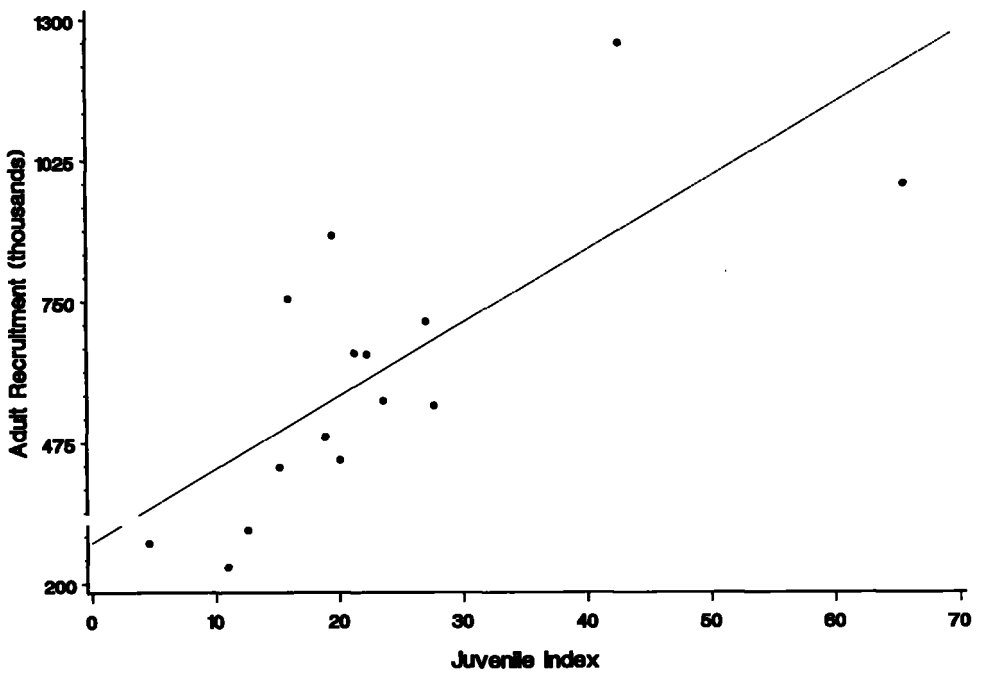

FIGURE 3.—Relationship between total adult recruitment (R_t) and the juvenile abundance indices (IND_t) of American shad from 1967 through 1982.

of the regression differed significantly from zero, indicating the presence of significant density-dependent mortality during the prejuvenile stage. When prejuvenile mortality rates were related to both egg production ($Eggs_t$) and mean June river flow, ($JFLOW_t$), the multiple regression model accounted for 80% of the variability in prejuvenile mortality (Table 3), and the slope estimates for egg production (b) and June flow (c) were positive and highly significant. Note that the standard error (SE) about the slope estimate (b) was reduced by 60% when June flow effects were considered. These results suggest that prejuvenile mortality rates are affected by a combination of density-dependent (egg production) and density-independent (June river flow) factors.

The mean density-dependent mortality rate during the prejuvenile phase ($Z_{D\,pre}$ = 1.18) from the multiple regression model was four times greater than the mean $Z_{D\,post}$ value (0.30) for postjuveniles (Table 3), suggesting that 80% (1.18/1.18 + 0.30) of the total compensatory reserve for American shad occurs before the juvenile stage. Whereas compensatory density-dependent mortality may play a significant role in regulating egg and larval abundance during years of high egg production, it is clear that most of the variability (82%) in egg and larval abundance is ascribed to density-independent factors.

Egg, Larval, and Juvenile Mortality, 1979–87

Analysis

To examine how larval and juvenile mortality rates varied with year-class strength, survivorship curves for 19,000–180,000 American shad larvae and 800–3,500 juveniles were developed annually from 1979 to 1987 following the techniques of Lough (1976) and Hewitt et al. (1985). Mortality rates could not be estimated directly for prolarvae because American shad yolk-sac larvae (7–9 mm TL) remain in deep water (Marcy 1976) and were only partially susceptible to the plankton seine.

All larvae and juveniles collected annually were separated into four length intervals: 1) 10–13 mm TL, reflecting first-feeding larvae with undeveloped pelvic fins (Wiggins et al. 1984); 2) 14–19 mm TL, associated with the onset of pelvic fin development (Lippson and Moran 1974); 3) 20–28 mm TL, representing larvae approaching metamorphosis, characterized by invagination of the gut (Maxfield 1953);

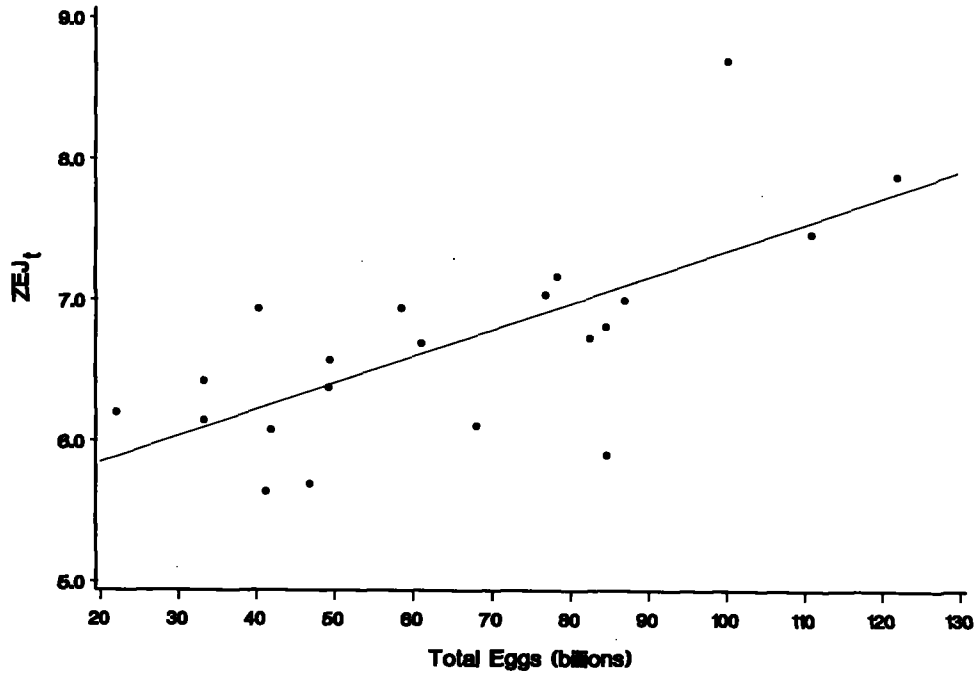

FIGURE 4.—Relationship between American shad prejuvenile mortality (ZEJ_t) and the number of eggs produced ($Eggs_t$) from 1967 through 1987.

and 4) 29–80 mm TL, corresponding to the juvenile stage and the onset of scale development (Marcy 1976). These four groups are hereafter referred to as early larval, midlarval, late larval, and juvenile stages, respectively.

We used otolith increment counts (Savoy and Crecco 1987) to age a subsample of 100–400 American shad larvae and 80–200 juveniles annually from 1979 to 1987. The age-length relationship for larvae and juveniles in all years was well described by the Gompertz growth equation (Crecco et al. 1983; Crecco and Savoy 1985b) so we used a pooled Gompertz equation to describe larval and juvenile growth. The average age (t) of each of the four length groups was estimated by rearranging the Gompertz equation:

$$t = \log_e[K/K - \log_e(L_t(L_0))]/a \quad (5)$$

where L_t = total length (mm); L_0 = length at hatching (8.0 mm); K = growth rate at the inflection point; and a = rate of exponential decay.

The daily instantaneous mortality rates (d) for each stage and their standard errors from 1979 through 1987 were estimated by an exponential model,

$$N_t = \mathrm{A}\ \exp(-dt), \quad (6)$$

that related abundance (N_t) and age (t) by nonlinear regression methods (SAS 1982). The total instantaneous mortality rates of early (ZEL_t), mid (ZML_t), and late (ZLL_t) larvae and juveniles (ZJ_t) were estimated by multiplying the corresponding daily mortality rate (d) by the average duration (Ds = days) within each stage. Previous studies (Crecco and Savoy 1985a; Savoy and Crecco 1987) found that the growth rates of early (10–13 mm) and midlarvae (14–19 mm) were positively correlated with June water temperatures, whereas the growth of late larvae and juveniles were independent of river temperatures. As a result, we adjusted the stage duration (Ds) of early and midlarvae with the mean June temperatures (U.S. Geological Survey 1979–87) from 1979 through 1987 and the larval growth-temperature equations (Crecco and Savoy 1985b: table 7).

We estimated total egg and prolarval mortality rates (ZE_t) indirectly from 1979 through 1987 by subtracting the sum of larval (ZEL_t, ZML_t, ZLL_t), juvenile (ZJ_t) and postjuvenile (ZA_t) mortality rates from the total prerecruitment mortality rate ($Z\mathrm{Total}_t$):

$$ZE_t = Z\mathrm{Total}_t - (ZEL_t + ZML_t + ZLL_t + ZJ_t + ZA_t), \quad (7)$$

where $Z\mathrm{Total}_t = -\log_e(R_t/\mathrm{Eggs}_t)$. However, since the 1983 through 1987 year classes have not been fully recruited to the spawning population, we estimated total adult recruitment (Rp_t) for those year classes by the following environment-dependent stock-recruitment model:

$$Rp_t = 24.29\ (PAR_t)\ \exp(-0.0052 \cdot P_b)\ \exp(-0.0032 \cdot P_a)\ \exp(-0.0025 \cdot J\mathrm{FLOW}_t) \quad (8)$$

Adult recruitment was estimated independently of the juvenile indices by substituting each year's parent stock size (PAR_t), mean June flow (JFLOW), female parent stock lifted over the Holyoke Dam (P_a), and female parent stock below the Holyoke Dam (P_b) (Table 1) into the model. This nonlinear model was shown (Lorda and Crecco 1987) to be a good predictor ($r^2 = 0.81$, $P < 0.001$) of adult recruitment (R_t) for the 1966 through 1982 year classes. Moreover, the predicted recruitment levels (R_t) of the 1983 through 1987 year classes from Equation (8) were closely correlated ($r = 0.92$, $P < 0.01$) with the corresponding juvenile abundance (J_t) for those years (Table 4) which is consistent with the positive correlation ($r = 0.78$, $P < 0.01$) between adult recruitment and the 1967–82 juvenile indices (Fig. 2). This justifies the use of Equation (8) to predict adult recruitment, total mortality, and postjuvenile mortality rates for the 1983–87 year classes.

The standard errors about the egg mortality rates (ZE_t) were derived as the sum of the variances of all other terms (Cochran 1965):

$$\mathrm{SE}_{ZE}^2 = \sqrt{\mathrm{SE}_{ZEL}^2 + \mathrm{SE}_{ZML}^2 + \mathrm{SE}_{ZLL}^2 + \mathrm{ZJ}^2 + \mathrm{SE}_{ZA}^2 + \mathrm{SE}_{Z\mathrm{Total}}^2} \quad (9)$$

The standard errors about the total prerecruitment ($Z\mathrm{Total}_t$) and postjuvenile (ZA_t) mortality rates (Table 5) were based on the same principle as Equation (9) (App. 1).

TABLE 4.—Predicted total adult recruitment of American shad from the environmental dependent stock-recruitment model (Equation (8)), 95% confidence limits about the recruitment values and juvenile abundance for the 1983–87 year classes.

Year	Predicted adult recruitment × 10^3	95% C.I.	Juvenile abundance × 10^3
1983	634	362–906	92,531
1984	196	112–280	45,738
1985	555	317–793	62,626
1986	587	335–839	59,811
1987	955	547–1,363	157,268

TABLE 5.—Estimates of the total ($Z\text{Total}_t$) and postjuvenile (ZA_t) instantaneous mortality rates and their standard errors (SE) for American shad from 1979 through 1987.

Year	$Z\text{Total}_t$	SE	ZA_t	SE
1979	10.94	0.26	4.36	0.23
1980	10.90	0.24	4.78	0.32
1981	11.26	0.25	4.31	0.25
1982	13.00	0.27	4.77	0.34
1983	11.80	0.30	4.98	0.36
1984	13.34	0.26	5.45	0.28
1985	12.21	0.29	4.72	0.28
1986	11.80	0.30	4.62	0.29
1987	10.80	0.28	5.10	0.47

Given that ZE represents total mortality throughout the egg and prolarval period, daily egg mortality rates were determined by dividing ZE by the average duration (Ds) of the egg and prolarval stages of American shad in the Connecticut River. Watson (1968) reported an inverse relationship between the incubation period (D) of shad eggs and water temperature (T) by the expression:

$$D = 120.95 \exp(-0.154 \cdot T). \quad (10)$$

To determine the duration (Ds) of the egg stage from 1979 through 1987 we substituted the mean June temperatures for the Connecticut River (U.S.G.S. Annual Water Year Reports 1979–87) into Equation (10).

The total number of prolarvae (age 2 days) and early larvae (age 10 days) for the 1979 through 1987 year classes was estimated by

$$NE_t = \text{Eggs}_t \cdot \exp(-ZE_t) \quad (11)$$

and

$$NF_t = \text{Eggs}_t \cdot \exp(-ZE_t - ZEL_t) \quad (12)$$

respectively, where NE_t is the estimated number of prolarvae larvae and NF_t is the number of early larvae. The abundance of older larvae and juveniles from each year class was estimated by adding their respective total mortality rates to Equation (12). To determine the life stage(s) at which year-class strength is established, we related the stage-specific total mortality rates and abundance estimates to the number of adult recruits (R_t or Rp_t) from the 1979–87 year classes in several linear models. If year-class strength is established early, there should be a significant positive correlation between the number of prolarvae (NE) and early larvae (NF) and adult recruitment, and total mortality rates during these early stages (ZE and ZEL) should be inversely related to adult recruitment.

To determine the extent of density-independent mortality at the egg, larval, and juvenile stages, we correlated the stage-specific total mortality rates from 1979 through 1987 to mean May and June river flows (m^3/s) and water temperatures (°C) in several linear models. May and June hydrographic and meteorological parameters were used because they coincide with egg, larval, and juvenile development in the Connecticut River (Leggett 1977) and were the only monthly abiotic variables that were significantly linked to adult shad recruitment from 1966 to 1980 (Crecco and Savoy 1984, 1987c). May and June water flows and temperatures were recorded by the U.S. Geological survey (U.S. Geological Survey 1966–1980) within the major spawning areas (river km 89) of American shad (Leggett 1977).

Results

The mean daily mortality rates from 1979 through 1987 declined by an order of magnitude from the egg through the juvenile stages (Table 6). Total egg mortality rates were relatively high (mean ZE = 2.584, cv = 18.5%) and were inversely correlated ($r = -0.76$, $P < 0.03$) with adult recruitment (R_t or Rp_t) from those year classes (Table 7). These data indicate that shad eggs and prolarvae (age 1–2 days) from 1979 through 1987 experienced high (85–96%) mortality that was directly linked to year-class success.

The total mortality rates (ZEL) among early larvae were slightly lower and more variable (mean ZEL = 1.608, cv = 31.5%) than the egg mortality rates (Table 6), and were also inversely related ($r = -0.83$, $P < 0.01$) to adult recruitment from 1979 through 1987. By contrast, the total mortality rates of older larvae (ZML and ZLL) and juveniles (ZJ)

TABLE 6.—Stage-specific total instantaneous mortality rates of egg, larval, and juvenile American shad from 1979 to 1987. SE = stage-specific standard errors; cv = coefficient of variation, Days = duration of each stage.

Year or statistic	Instantaneous total mortality									
	Egg + pro-larvae (day 2)		Early larvae (day 3–9)		Mid-larvae (day 10–18)		Late larvae (day 19–29)		Juvenile (day 30–100)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
1979	2.481	0.554	1.323	0.245	1.116	0.189	0.330	0.110	1.330	0.280
1980	1.853	0.819	1.218	0.186	1.096	0.336	0.693	0.099	1.260	0.280
1981	2.580	0.684	1.836	0.108	0.408	0.328	0.726	0.154	1.400	0.210
1982	2.940	0.501	2.144	0.152	1.160	0.210	0.726	0.187	1.260	0.210
1983	3.012	0.785	1.400	0.546	0.522	0.234	0.836	0.143	1.050	0.140
1984	2.706	0.601	2.520	0.352	0.640	0.330	0.484	0.242	1.540	0.280
1985	---------- NO DATA ----------								1.330	0.280
1986	3.158	0.652	1.323	0.196	1.206	0.261	0.374	0.066	1.120	0.280
1987	1.944	0.852	1.098	0.180	0.864	0.128	0.464	0.088	1.330	0.210
Z	2.584		1.608		0.877		0.579		1.286	
SE	0.169		0.179		0.111		0.066		0.051	
cv	0.185		0.315		0.359		0.325		0.120	
Days	7.2		6.9		8.9		11.0		70.0	
Daily Z	0.359		0.233		0.099		0.053		0.018	

TABLE 7.—Correlations between stage-specific total mortalities and adult recruitment and several abiotic factors from 1979 to 1987 for American shad. P = probability levels.

Stage	Adult recruitment	May flow	May temperature	June flow	June temperature
Egg	−0.76	0.38	−0.08	0.66	−0.59
P	0.03	0.35	0.85	0.08	0.13
Early	−0.83	0.42	−0.21	0.81	−0.64
P	0.01	0.29	0.62	0.01	0.09
Mid	0.16	−0.41	0.49	0.09	−0.34
P	0.71	0.32	0.22	0.83	0.42
Late	−0.02	0.20	−0.51	−0.13	0.18
P	0.96	0.64	0.20	0.75	0.68
Juv	−0.19	0.05	0.02	0.26	−0.08
P	0.65	0.91	0.97	0.53	0.86

were highly variable, but showed no relationship to adult recruitment.

Given that high (94–99%) egg and early larval mortality rates were inversely related to year-class strength, the abundance of first-feeding larvae (age 10 days) was closely correlated ($r = 0.84, P < 0.01$) with adult recruitment (Rp_t) from 1979 through 1987 (Table 8). Because year-class strength from 1967 through 1987 was independent ($r = -0.15, P < 0.46$) of egg production ($Eggs_t$), our results suggest that year-class strength of American shad is determined by the number of shad that survive the embryonic and early larval stages.

Early larval mortality rates from 1979 to 1987 were positively correlated with mean June river flows. No such relationships were evident for any other stage-specific mortalities (Table 7). The high egg and early larval mortality rates (Table 6) and relative failure of the 1982 and 1984 year classes coincided with major storm events in mid-June 1982 and late May 1984 (Crecco and Savoy 1984) which increased river flows and kept water temperatures below 17°C until late June. The high river flows in 1982 and 1984 were also coupled with the highest parent stocks on record since 1967 (Table 1). By contrast, the relatively low egg and early larval mortality rates for the dominant 1980 and 1987 year classes were associated with low June river flows, a steady rise in June water temperatures (Crecco and Savoy 1984) and low to moderate size parent stocks (Table 1). These results suggest that dominant year classes of American shad are most likely to occur when lower than normal June flows are coupled with relatively small spawning stocks.

Prejuvenile Density-Dependent Mortality: A Closer Look

Analysis

Having estimated that 82% of the density-dependent mortality for American shad takes place before the juvenile stage (Table 3), we attempted to estimate the relative contribution of density-dependent mortality during the egg, early, mid-, and late larval and juvenile stages from 1979 through 1987. We related egg mortality rates (ZE_t) from

TABLE 8.—Relationship between the number ($\times 10^6$) of American shad at each life history stage and adult recruitment from each year class. r = correlation coefficient and P = probability levels from 1979 to 1987.

Year-class	Stage						
	Egg	Pro-larvae	Early larvae	Mid-larvae	Late larvae	Juvenile	Adult[1]
1979	496	41.5	11.0	3.6	2.6	0.7	882
1980	682	106.9	31.6	10.6	5.3	1.5	1,256
1981	586	44.4	7.1	4.7	2.3	0.6	758
1982	1,002	53.0	6.2	1.9	0.9	0.3	282
1983	846	41.6	10.3	6.1	2.6	0.9	634
1984	1,220	81.5	6.6	3.5	2.1	0.5	196
1985	1,110	----------		NO DATA		----------	555
1986	784	33.3	8.9	2.7	1.8	0.6	587
1987	470	67.3	22.4	9.5	5.9	1.6	955
r =	−0.15[2]	0.33	0.84	0.80	0.79	0.82	
P =	0.46	0.43	0.01	0.02	0.02	0.01	

[1]Predicted or observed recruitment in thousands.
[2]Correlation coefficient for egg abundance and recruitment was based on the 1967–87 data (Tables 1, 2).

1979 to 1987 to total egg production (Eggs_t) in a linear model:

$$ZE_t = a + b(\text{Eggs}_t). \quad (13)$$

As before, significant density-dependence would be shown if the slope (b) in Equation (13) was positive and differed significantly from zero.

The cumulative amount of density-dependent mortality during the egg and early larval stages combined was estimated by summing the instantaneous total mortality rates of early larvae (ZEL_t) and eggs (ZE_t) and then regressing the total ($ZE_t + ZEL_t$) against egg production as in Equation (13). This procedure was repeated for each subsequent stage by adding their respective instantaneous total mortality rates. We then estimated the relative magnitude of density-dependent mortality (Z_D) at each stage by multiplying the slope (b) of each regression equation by the geometric mean egg production ($G\text{Egg}$) from 1967 through 1987. The density-independent mortality rate (Z_I) at each stage was expressed by the y-axis intercept (a) of each regression equation. The percentage contribution of density-dependent mortality ($\%Z_D$) for each period was the ratio of Z_D to total mortality ($Z_D + Z_I$) times 100.

Results

Our results showed that significant density-dependent mortality first occurs during the early larval stage and persists for all stages thereafter (Table 9). The percentage contribution of density-dependent mortality ($\%Z_D$) rose from 24% of the total during the egg stage to 41% during the early larval stage, and then declined during the mid- and late larval stages as the magnitude of density-independent mortality increased. The mean density-dependent mortality rate for the egg and early larval

TABLE 9.—Relationship between the cumulative mortality rates and parent stock sizes (Eggs_t). The cumulative mortality rate was egg mortality (ZE) plus early larval mortality ($Z2$), midlarval mortality ($Z3$), late larval mortality ($Z4$), and juvenile mortality ($Z5$). Z_D = density-dependent mortality rate, Z_I = density-independent mortality rate, $\%Z_D$ = percentage density-dependent mortality, $\%Z_I$ = percentage density-independent mortality, t = student t-statistic.

Model	b parameter	SE(b)	t	Z_D	Z_I	$\%Z_D$	$\%Z_I$
$ZE = a + b(\text{Eggs}_t)$	9.89×10^{-9}	6.40×10^{-9}	1.55	0.59	1.83	24	76
$Z2 = a + b(\text{Eggs}_t)$	2.57×10^{-8}	7.76×10^{-9}	[1]3.31	1.54	2.24	41	59
$Z3 = a + b(\text{Eggs}_t)$	2.44×10^{-8}	8.16×10^{-9}	[1]2.99	1.46	3.21	31	69
$Z4 = a + b(\text{Eggs}_t)$	2.60×10^{-8}	7.74×10^{-9}	[1]3.36	1.55	3.67	30	70
$Z5 = a + b(\text{Eggs}_t)$	2.69×10^{-8}	7.50×10^{-9}	[1]3.59	1.61	4.88	25	75

[1]Significant student t-statistic at the $P < 0.01$ level and SE(b) = standard error of b.

stages combined (Z_D = 1.54) between 1979 and 1987 was not significantly different (Table 9) from the total density-dependent mortality rate ($Z_{D\,pre}$ = 1.18) estimated during the prejuvenile period from 1967 to 1982 (Table 3), suggesting that nearly all of the density-dependent mortality for prejuvenile American shad occurs before the midlarval stage.

DISCUSSION

Although American shad eggs and early larvae experience high mortality (15–40%/day) in the Connecticut River, the average density-dependent mortality rate ($Z_{D\,pre}$ = 1.18) during those stages comprised a relatively small percentage (18%) of the total prerecruitment mortality. This suggests that most of the annual variability in American shad recruitment is explained by density-independent factors, which is consistent with the significant positive correlation between mean June flow and egg and early larval mortality rates, and with the significant inverse correlation ($r = -0.74$, $P < 0.001$) between mean June river flow and adult recruitment from the 1967 through 1982 year classes (Crecco and Savoy 1984, 1987b). Whereas these data illustrate that density-dependent mortality plays a minor role in governing annual variability in American shad recruitment, this does not mean that compensatory processes are trivial. As pointed out by Ricker (1954) and others (Cushing 1974; Garrod and Horwood 1984), only a small amount of density-dependent mortality is required to stabilize the growth potential of fish populations because density-dependent effects become progressively more effective at higher egg and larval densities (Shepherd and Cushing 1980; Murray 1982).

Although our results on American shad support the Gulland (1965) hypothesis that density-dependent mortality persists throughout the prerecruitment period, most (82%) of the density-dependent mortality occurs during the egg and early larval stages. Our average estimate of density-dependent mortality (Z_D = 1.54) during the early larval periods does not differ significantly from the mean Z_D value (1.34) estimated among the 5-d larval cohorts in 1983 and 1984 (Crecco and Savoy 1987a), or from the mean density-dependent mortality rate Z_D (1.21) estimated by stock-recruitment methods for the entire prerecruitment period (Lorda and Crecco 1987). That year-class strength is established early in the ontogeny of American shad is supported further by the significant positive correlation (r = 0.84, $P < 0.009$) between the relative abundance of early larvae and all subsequent stages from 1979 through 1987 and adult recruitment from those year classes (Table 8).

The main causes of density-dependent mortality are thought to be predation, competition, and cannibalism (Ricker 1954). Since adult American shad are not thought to feed in freshwater (Walburg and Nichols 1967), we can probably eliminate cannibalism as a mechanism for significant density-dependent mortality during the egg and early larval stages. Therefore, density-dependent mortality among early American shad larvae is most likely caused by intraspecific competition for food or space and predation. The exact underlying density-dependent mortality mechanisms are difficult to quantify because the outcome of competition and predation may depend on June flow effects shown here (Table 3) and elsewhere (Crecco and Savoy 1987a, b) to be the principal density-independent factor. High June river flows have been shown to reduce June river temperatures (Crecco and Savoy 1984) and the growth rates of shad eggs (Watson 1968) and early larvae (Crecco and Savoy 1985b). Because slower growing larvae may be susceptible to predation for a longer period of time (Hunter 1976), periods of high flow may indirectly enhance egg and larval predation. Additionally, since high flows reduce the spatial patchiness (Crecco and Savoy 1987a), abundance and availability of river zooplankton (Whitton 1980; Threlkeld 1986), high flows may result in increased levels of competition among American shad larvae for available prey, especially if shad larvae are capable of depleting local aggregations of edible zooplankton. Periods of high runoff that coincide with peak larval production, such as in June 1982 and 1984, may advect larvae and their zooplankton prey from eddies and backwaters where they are normally found (Cave 1978) to areas of high predator abundance. In light of the many ways in which June flows potentially mediate larval mortality, it is unlikely that a single compensatory mechanism is responsible for the relatively high density-dependent mortality rate ($Z_{D\,pre}$) among early larvae.

Since egg and prolarval shad have endogenous food reserves, density-dependent mortality of these stages is likely due to predation and competition for sites among spawning adults. As spawning stocks reach high densities, such as in 1982–84, crowding of adult fish on the spawning grounds may result in a reduction in the number of eggs released (Goodyear 1980). In addition, since the amount of spawning habitat in the Connecticut River can be considered fixed from year to year, larger spawning stocks are more apt to deposit an increasing percentage of eggs in unfavorable areas. Layzer (1974)

noted that the highest survival rates of American shad eggs occurred over gravel and rubble substrates. Since these areas generally have higher water velocities, eggs lodged within the interstices of the gravel and rubble are less likely to be eaten by predators or covered by silt. Dense aggregations of eggs may also be highly susceptible to fungal agents (Leach 1925), which could then act as efficient density-dependent predators. However, since predators of American shad eggs and larvae in the Connecticut River have not yet been identified, density-dependent losses are difficult to quantify. Also, predation mortalities in general may be either density-dependent or density-independent, depending on the functional response between the predator and the prey (Hassell 1978), and whether predators actively search for discrete aggregations of eggs and larvae or prey on randomly encountered eggs and larvae (Gulland 1987).

In the absence of direct egg mortality estimates of American shad, the accuracy of our egg mortality estimates (ZE_t) from Equation (7) are difficult to evaluate, particularly since the standard errors about the estimates are highly variable (Table 6). To provide an independent estimate of daily egg mortality, we used the multiple regression method of McGurk (1987) to estimate the average daily egg mortality rate. This method requires an estimate of the patchiness and the mean dry weight of a shad egg. We derived Lloyd's patchiness index ($\bar{x}$ = 7.26, SE = 0.376) for American shad eggs in the Connecticut River from the 1974–75 egg surveys in the Holyoke Dam impoundment (NUSCo 1977). Substituting the mean weight of a shad egg (0.00025 g, Leggett 1969) and the mean patchiness index into McGurk's equation 4, yields an instantaneous daily egg mortality rate of 0.34 which closely approximates our average estimate (0.36) from 1979 to 1987 (Table 6).

Lastly, since it is presently unknown if younger (smaller) virgin female American shad produce smaller, less viable eggs than older shad as was reported for cod, *Gadus morhua*, (Knutsen and Tilseth 1985), the contribution of the age structure to the parent progeny relationship (Rosenberg and Doyle 1986) should be considered. This issue and an examination of whether egg deposition rates are density-dependent should be addressed by monitoring egg retention rates among postspawning American shad.

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APPENDIX 1

The total prerecruitment ($Z\text{Total}_t$) and postjuvenile (ZA_t) mortality rates from 1979 through 1987 were estimated by

$$Z\text{Total}_t = -\log_e(Par_t * 200{,}000) - \log_e(R_t)$$

and

$$ZA_t = \log_e(J_t) - \log_e(R_t),$$

respectively. The standard errors about $Z\text{Total}_t$ and ZA_t were estimated as the sum of the variances (Cochran 1965):

$$\text{SE}_{Z\text{Total}_t} = \sqrt{\frac{S^2_{R_t}}{n_t} + \frac{S^2_{Par_t}}{n_t}}$$

and

$$\text{SE}_{ZA_t} = \sqrt{\frac{S^2_{J_t}}{n_{J_t}} + \frac{S^2_{R_t}}{n_t}}$$

respectively. The variance estimates ($S^2_{R_t}$, $S^2_{Par_t}$) of adult recruitment and spawning stock size were calculated from the log transformed estimates from the daily lift rates at the Holyoke Dam, where n_t is the total number of days in which 99% of the American shad were lifted. The variance ($S^2_{J_t}$) about the juvenile abundance estimates (J_t) was based on the log transformed catches per seine haul from all stations and collection dates, where n_{J_t} is the total number of seine hauls made in that year.

METABOLIC RESPONSES OF SPOT, *LEIOSTOMUS XANTHURUS*, AND ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, LARVAE TO COLD TEMPERATURES ENCOUNTERED FOLLOWING RECRUITMENT TO ESTUARIES

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ABSTRACT

The larvae of marine fishes that spawn during fall-winter in coastal North Carolina waters experience a decrease in temperature as they enter estuarine nursery areas. To determine the effect of changes in temperature on larval metabolism, the oxygen consumption of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, was measured and their $Q0_2$ and Q_{10} values were determined. Atlantic croaker respiration decreased with temperature at rates that would be expected if no compensation or stress were involved. Spot showed unexpectedly high respiration rates at low temperature. The increased respiration is apparently due to stress. Based on laboratory feeding and growth data, we concluded that spot are subject to an energy deficit at ≤10°C. We infer the timing of larval immigration corresponds with environmental temperatures reaching tolerable levels. Atlantic croaker larvae immigrate earlier in the winter and are exposed to cold water for longer periods than spot larvae. Our conclusion is that stress and energy loss experienced by early immigrating spot larvae may result in increased mortality.

The larvae of fishes that spawn during fall and winter in offshore North Carolina waters experience a decrease in both temperature and salinity as they enter estuarine nursery areas (Fig. 1). The spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, two sympatric species of Sciaenidae, are representative of winter spawning species off the North Carolina coast.

Previously, we have examined the effects of increased temperature on the oxygen and food consumption of the postlarval stages of these two species (Hoss et al. 1971, 1974; Peters and Kjelson 1975). In this paper we continue our research on the early life history of these species and evaluate how decreasing water temperature, encountered following recruitment into estuarine waters, might affect oxygen consumption, food consumption, and ultimately survival.

Crawshaw et al. (1981) stated that young fish typically select warm shallow water because 1) it permits more rapid growth owing to higher metabolism, given an adequate food supply, and 2) the predation by larger fish is less in shallow water. For some fish this explanation is plausible, but this does not apply to the larvae of many winter-spawning marine fishes which begin life in relatively warm coastal waters and then enter colder estuarine waters. For these species we expect that metabolism and growth of the estuarine immigrants should be reduced (Brett 1956). The specific objective of this paper is to describe how decreasing temperature affects the metabolism of larval fish as they are moved from warm to cold water by a combination of passive and active transport mechanisms that are not, as yet, completely understood. Oxygen consumption is a common method of estimating metabolic activity, which frequently changes in response to environmental conditions (O'Hara 1968). In this study we measured routine oxygen consumption which is the amount used by fish whose only movements are spontaneous.

STUDY AREA AND METHODS

Spot and Atlantic croaker spawn off the North Carolina coast inshore of the Gulf Stream over the continental shelf (Hildebrand and Cable 1930; Dawson 1958; Powles and Stender 1978). Here, spot spawn from October to February, but principally from December to January while Atlantic croaker spawn from September to May but principally between October and December (Lewis and Judy 1983). After between 30 and 60 days in coastal

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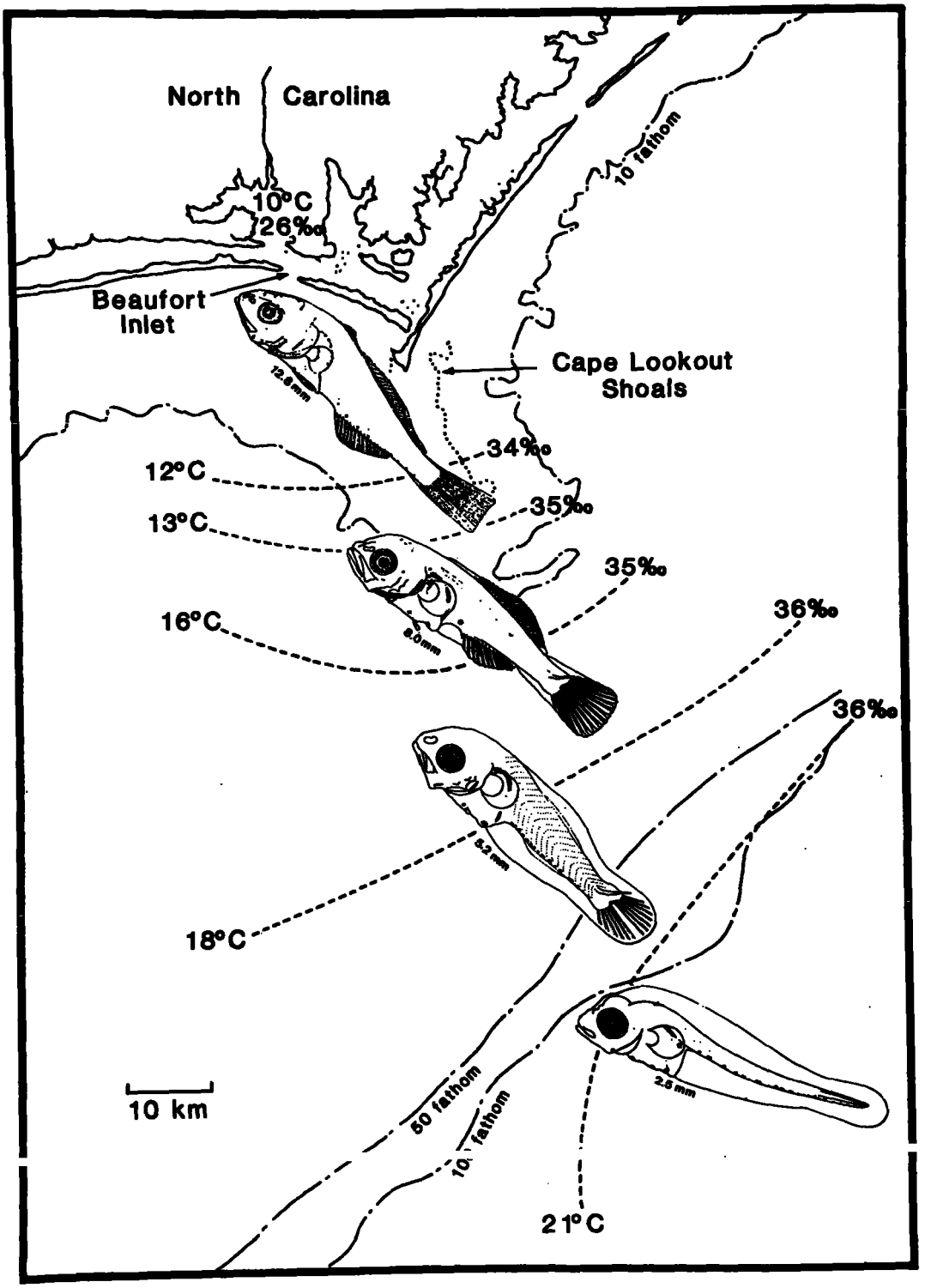
North Carolina
10°C
26‰
Beaufort Inlet
10 fathom
Cape Lookout Shoals
34‰
12°C
35‰
13°C
35‰
16°C
36‰
36‰
18°C
10 km
50 fathom
10 fathom
21°C

waters (Warlen 1982; Warlen and Chester 1985), the larvae enter estuaries where they develop into juveniles. In the spawning area, water temperatures are usually between 18° and 25°C (Fahay 1975; Hettler and Powell 1981). The fish encounter decreasing temperatures as they move inshore to the estuarine nursery areas. In the lower Newport River estuary, for example, mean water temperatures between November and March may range from 14° to 6°C with the highest temperatures during this period occurring in November and the lowest in January (Hoss 1974).

Larvae of Atlantic croaker and spot were obtained from both field collections and eggs spawned in the laboratory. Older larvae were captured in a bridge net (Hettler 1979) and held in the laboratory for no more than a week prior to use. First feeding larvae were obtained from spawned fish, reproduced by the methods of Hettler and Powell (1981), and then were reared at experimental temperatures.

Oxygen consumption was measured with a differential respirometer (Umbreit et al. 1964), following procedures used by Hoss, Hettler, and Coston (1974). Fish were transferred to 15 mL respiration flasks and, following a 2-h acclimation period, their oxygen consumption was measured. Numbers of larvae per flask varied between 1 and 30, depending on the size of the larvae. Acclimation temperatures were 10°, 15°, and 20°C. Notochord or standard lengths and dry weights were obtained for individual fish.

The metabolic equation $Q = aW^k$, was used to describe the relation between oxygen consumption and dry weight of fish acclimated at 10°, 15°, and 20°C. In this equation, W is the weight of the fish, and a and k are constants for the species obtained from least-squares regression of the log of oxygen consumption on the log of weight (Winberg 1956). A k value of 0.67 implies that oxygen consumption varies in proportion to surface area, whereas a value of 1 indicates that respiration varies in proportion to weight.

We used the metabolic equation to estimate oxygen consumption of larvae of equal weight at different temperatures. We compared larvae of 4 mg dry weight because this is the realistic estimate of their weight as they are transported from coastal to estuarine waters (Warlen 1982; Warlen and Chester 1985).

Growth and feeding rates of small spot (≃20 mm SL) collected from the Newport River were calculated from data collected in the laboratory at several temperatures. Wet weights (≃15–30 mg) were recorded to the nearest milligram, and 10 fish were randomly assigned to 4 L test and control containers. Control fish were dried to determine the dry/wet weight ratio, which was then used to estimate initial dry weight of experimental fish. One experiment was conducted at 6°, 8°, 10°, 12°, and 16°C, and two experiments were conducted at 18°C. In all cases fish were fed newly hatched brine shrimp several times a day to assure an ad libitum food supply. After 4–6 days all food was removed; larvae were allowed time to clear their guts and then were dried and weighed.

Growth and feeding rates were expressed as percent of body weight per day. Growth rate was calculated from the expression:

$$\text{Growth rate} = 100\,[(Wn/Wo)^{1/n} - 1]$$

where Wn = dry weight of all fish in a tank at day n
Wo = estimated original dry weight of fish
n = number of days fed.

Calculation of feeding rates required the assumption of constant growth rates. Using original dry weights and calculated growth rates we determined the total dry weight of fish in each container at the beginning of each day. Dry weights of brine shrimp eaten each day divided by the calculated dry weights of fish gives proportion of body weight ingested. These proportions were then summarized as average daily percent of dry body weight ingested.

In order to compare metabolic parameters, i.e., oxygen consumption, feeding, and growth rates, the following conversion factors were used: 1.0 mg dry wt = 5.0 cal (Thayer et al. 1973; Paffenhöffer 1967); 1.0 mg O_2 = 3.38 cal (Phillipson 1966) and 0.7 mg O_2 = 1 mL O_2 at STP. One tenth calorie per fish per day was added to all the rates so that measured zeros could be shown on a log scale.

RESULTS AND DISCUSSION

The regression equations relating oxygen consumption to weight at several temperatures are shown in Table 1. Higher coefficient of determination (R^2) values were found at higher temperatures, a trend best explained by differences in the size range of fish measured at different temperatures. Values for k, were generally comparable to values reported by other investigators for fish of a similar size and at comparable temperatures—Hoss (1974), pinfish; Houde and Schekter (1983), bay anchovy, sea bream, and lined sole; Almatar (1984), herring; and Laurence (1978), cod and haddock.

TABLE 1.—Metabolic equations relating oxygen consumption to body size. $Q = aW^k$ where Q = oxygen consumption ($\mu L\ O_2 \cdot h^{-1}$), *a* and *k* are regression coefficients, W is dry wt in mg, N is the number of observations, T the temperature, and R_2 the coefficient of determination.

Species	T	N	W	*a*	*k*	R^2
Atlantic croaker	10	52	1.50 - 6.43	1.80	0.66	0.42
	15	65	1.90 -11.71	2.00	1.02	0.65
	20	81	0.013- 9.31	3.59	0.86	0.94
Spot	10	37	1.82 - 8.01	3.63	0.70	0.54
	15	48	2.18 -10.27	3.15	0.64	0.63
	20	79	0.014- 8.91	4.07	0.92	0.97

Comparing between measured oxygen consumption rates at 10° and 15°C and those predicted from Van't Hoff's equation (Vernberg and Vernberg 1972), we conclude that Atlantic croaker show no sign of regulating their oxygen consumption as water temperature is decreased. The difference between oxygen consumption rates based on Q_{10} values of 2 and 3 (Fig. 2) is an expected range. For every 10°C change in temperature, the rate of a chemical reaction typically changes by a factor of 2 to 3. A Q_{10} value of appreciably <2 or more than 3, indicates that some process other than a chemical one is involved (e.g., a change in cell membrane permeability). A Q_{10} of one indicates temperature independence (Vernberg and Vernberg 1972). Our conclusion that Atlantic croaker did not display thermal stress is based on the fact that measured respiration rates at reduced temperatures (10° and 15°C) were within the range expected (Fig. 2A).

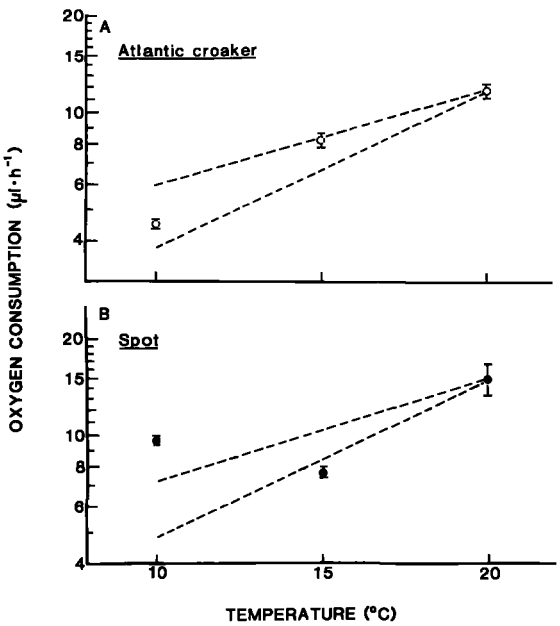

FIGURE 2.—Oxygen consumption rates for 4 mg Atlantic croaker (A) and spot (B) at three temperatures estimated from equations in Table 1. The bars indicate standard errors from regressions in Table 1. Broken lines are estimates of the rates expected based on Van't Hoff's equation, the rate measured at 20°C, a Q_{10} of 2 (upper line) and a Q_{10} of 3 (lower line).

For spot a decrease in temperature from 20° to 15°C resulted in a decrease in oxygen consumption of approximately the amount expected for a Q_{10} of 3. A further decrease in temperature to 10°C, however, caused an increase in the respiration rate. The changes in oxygen consumption at low temperatures could be interpreted either as adaptive, i.e., maintaining a high metabolic rate even at the lower temperature, or inadaptive, i.e., a metabolic breakdown.

Based on feeding, growth, and survival data, however, we think the increase in respiration by spot at 10°C is a result of cold stress, not adaptation. In Figure 3 we present three measures of metabolic rate, ad libitum feeding rate, maximum growth rate, and routine oxygen consumption for spot, all as a function of temperature. Feeding, growth, and oxygen consumption rates decrease with decreasing temperature and the rates are similar over a limited range of the conditions tested (Fig. 3). The rates of decline in feeding and growth from 18° to 12°C approximates that of oxygen consumption from 20° to 15°C. At lower temperatures stress appears to become important. For example, it was not possible to measure growth at 10°C or below because only a fraction of the larvae survived. At 8° and 10°C some of the larvae did not eat and at 6°C none of them did. This agrees with Dawson (1958) who concluded that the lethal minimum temperature for spot is in the 4.0°-5.0°C range and probably varies with size. The intersection of ad libitum feeding rate and routine oxygen consumption occurs at approximately 10°C (Fig. 3). At this temperature there is just enough energy available for routine metabolism. Below this temperature there is not enough energy available even at the ad libitum feeding rate to maintain the larvae, and spot held at this temperature for any length of time would be unlikely to survive.

We conclude from our data on metabolic responses to temperature that spot and Atlantic croaker larvae differ in their response to cold temperatures which prevail at the time of their recruitment to the estuary and that this difference may have important implications for their survival. Both species spawn in warm waters of the continental shelf where the eggs hatch. As the larvae grow they are

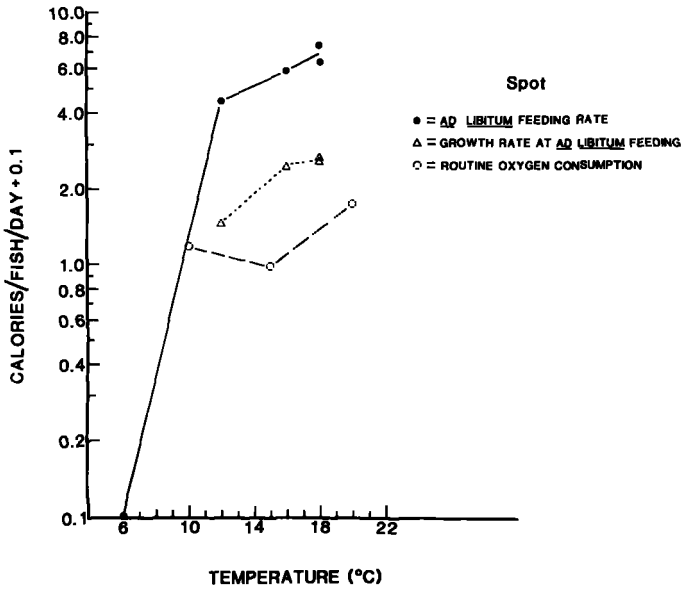

FIGURE 3.—Ad libitum feeding rate, growth rate at ad libitum feeding rate, and routine oxygen consumption for 4 mg dry wt spot at various temperatures between 6° and 20°C.

transported from warm coastal waters into cold estuarine waters. Atlantic croaker are capable of enduring low winter temperatures with decreased metabolic rates that allow for balanced energy intake. Spot, in contrast, show signs of thermal stress manifested as increased respiration rate (at 10°C). This increased metabolism along with no attendant increase in feeding results in an energy deficit and in eventual mortality of the larvae. Species specific differences in the time of entry to the estuary serves as ecological evidence supporting our contention that spot are more susceptible to cold weather. Most spot enter the estuary after the peak in Atlantic croaker immigration and generally after the coldest weather.

Our findings have important implications with respect to recruitment of estuarine-dependent fish which spawn in the ocean during winter. It may be that during severe winters, many of the larvae of cold sensitive species (e.g., spot) that reach the estuary early are killed by cold water temperatures (10°C or less). Thus, only the late arriving larvae survive to recruit into the fishery. The difference in survival between severe and normal winters may help to explain in part the difference between good and poor year classes of certain fish.

Acknowledgments

We thank W. Hettler for providing eggs of laboratory spawned fish, and W. Hettler and J. Govoni for providing critical reviews of the manuscript. This research was funded in part by a cooperative agreement between the National Marine Fisheries Service and the Department of Energy E(49-7)5.

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GROWTH OF PACIFIC SAURY, *COLOLABIS SAIRA*, IN THE NORTHEASTERN AND NORTHWESTERN PACIFIC OCEAN[1]

YOSHIRO WATANABE,[2] JOHN L. BUTLER,[3] AND TSUKASA MORI[4]

ABSTRACT

Growth of the Pacific saury, *Cololabis saira*, from the northeastern and northwestern Pacific Ocean was studied using otolith growth increments. We found that growth of Pacific sauries from the western Pacific was higher than that from the eastern Pacific. Assuming that otolith growth increments are deposited daily, average growth rates from hatching up to 1 year old were 0.62 mm/d in the eastern and 0.85 mm/d in the western Pacific. Because the growth rate changes at around 100 mm, two curves were used to model the growth of Pacific saury in the western Pacific: one for fish up to 100 mm and the other for fish larger than 100 mm. Based on counts of daily increments, Pacific sauries may be short lived. The oldest specimen examined was only 14 months old.

The Pacific saury, *Cololabis saira* (Brevoort), is distributed throughout the North Pacific Ocean and is one of the most important commercial fishes in the northwestern Pacific. The average annual catch of Pacific saury in Japan has been approximately 200,000 t (metric tons) in the last 20 years (Statistics and Information Department, Japan 1985). The catch has varied by an order of magnitude in the last 20 years from a minimum of 63,000 t in 1969 to a maximum of 406,000 t in 1973. Fluctuation in stock size is a major factor in catch variability although economic factors such as fish price may also affect total landings. However, the causes of stock fluctuation in the western Pacific remain unknown. In the eastern Pacific, the Pacific saury has not been exploited but is recognized as a potential fishery resource (Ahlstrom 1968; Smith et al. 1970).

Investigations of the Pacific saury have mainly been devoted to such subjects as systematics, abundance, distribution, migration, and formation of fishing ground in relation to oceanographic conditions (e.g., Hubbs and Wisner 1980; Smith et al. 1970; Odate 1977; Fukushima 1979; Sablin and Pavlychev 1982; Gong 1984). Age determination and growth, however, remain controversial (Hatanaka 1955; Hotta 1960; Novikov 1960; Sunada 1974; Kim and Park 1981), notwithstanding their critical importance for fish stock assessment.

The discovery of daily increments in the otoliths of fishes (Pannella 1971) has made it possible to estimate age and growth of larval and juvenile fishes accurately. Daily increments have been used to age many species of fishes (Jones 1986). Nishimura et al. (1985) reported the presence of growth increments in Pacific saury otoliths observed by scanning electron microscopy and suggested that it is possible to estimate age and growth of Pacific saury by using daily increments in the otolith. The purpose of this paper is to determine the age of Pacific sauries from the eastern and western North Pacific using daily increments and to compare the growth rates in these areas.

MATERIALS AND METHODS

We read otoliths of 75 Pacific sauries from the northeastern and 172 from the northwestern Pacific Ocean. Details of sampling and methods of reading otoliths are summarized in Table 1 and Figure 1. Additional samples from the western Pacific were used to determine the relation between otolith size and fish length. Fish from the eastern Pacific were fixed and preserved in 80% alcohol after capture, and those from the western Pacific were stored frozen and thawed when processed. Because specimens frequently have damaged upper jaws, knob length (the distance from the tip of the lower jaw to the posterior end of the muscular knob at the base of a caudal peduncle) is the standard measure of body size in Pacific saury. All body lengths in this paper are knob length.

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TABLE 1.—Collection records of saury samples from the eastern (# 1–10) and the western (# 11–22) North Pacific. N = Neuston net; G = Gill net; D = Dip net.

Sample	Date	Location		No.	Size range (KnL mm)	Gear	Micro-scope
		Lat.	Long.				
1	80 06 29	36°02'N	124°04'W	10	19.8–109.0	N	LM
2	80 06 29	36°07'N	123°55'W	10	19.8– 66.0	N	LM
3	80 06 29	36°07'N	123°45'W	10	15.3– 96.0	N	LM
4	81 10 26	46°36'N	127°49'W	5	47.8–235.0	N	LM
5	81 10 27	47°19'N	126°09'W	6	38.0–142.0	N	LM
6	81 10 28	47°20'N	124°30'W	12	23.9–216.0	N	LM
7	81 10 29	46°21'N	127°38'W	1	209.0	N	LM
8	81 10 30	46°38'N	125°54'W	14	20.6– 85.0	N	LM
9	81 11 01	45°21'N	127°38'W	4	27.0– 71.0	N	LM
10	81 11 02	45°38'N	124°51'W	3	70.0–206.0	N	LM
11	84 05 26	37°01'N	164°02'E	19	145.0–230.0	G	SEM
12	84 06 02	37°00'N	158°00'E	114	38.0–125.0	N	SEM
13	84 07 16	42°00'N	172°00'E	7	213.0–282.0	G	SEM
14	84 10 06	43°09'N	153°14'E	5	300.0–330.0	D	SEM
15	85 05 20	36°00'N	150°00'E	3	21.0– 69.5	N	LM
16	85 05 21	38°15'N	149°59'E	2	8.3– 12.5	N	LM
17	85 05 23	38°30'N	152°00'E	2	26.5– 45.5	N	LM
18	85 05 24	38°00'N	152°00'E	9	29.0– 85.0	N	LM
19	85 05 29	38°45'N	156°00'E	3	16.0– 33.5	N	LM
20	85 05 29	38°30'N	156°00'E	2	27.0– 33.0	N	LM
21	85 05 29	38°15'N	156°00'E	3	24.6– 65.0	N	LM
22	85 05 30	38°00'N	156°00'E	3	31.5– 68.5	N	LM

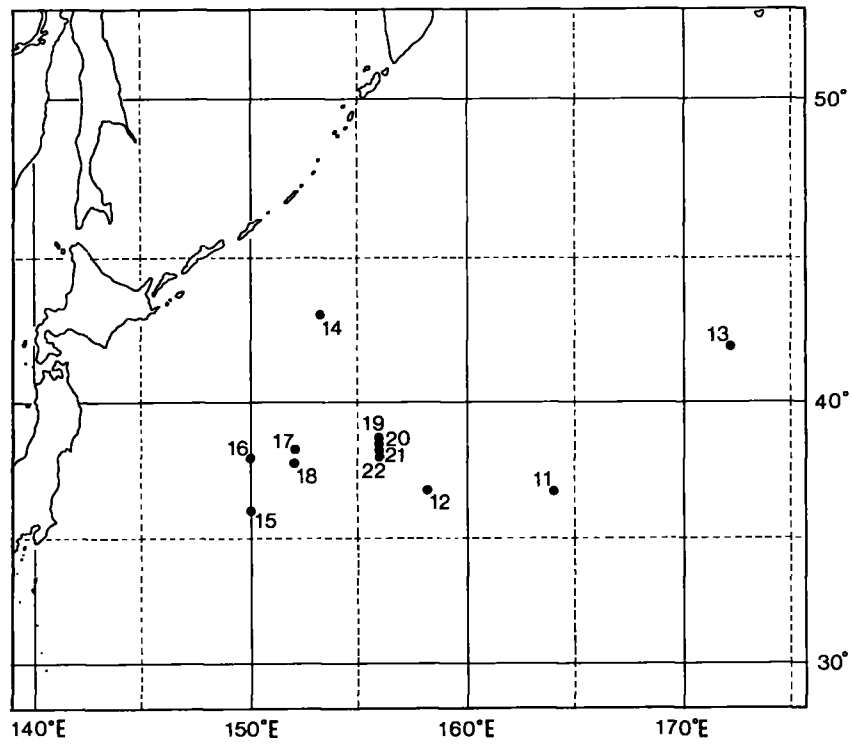


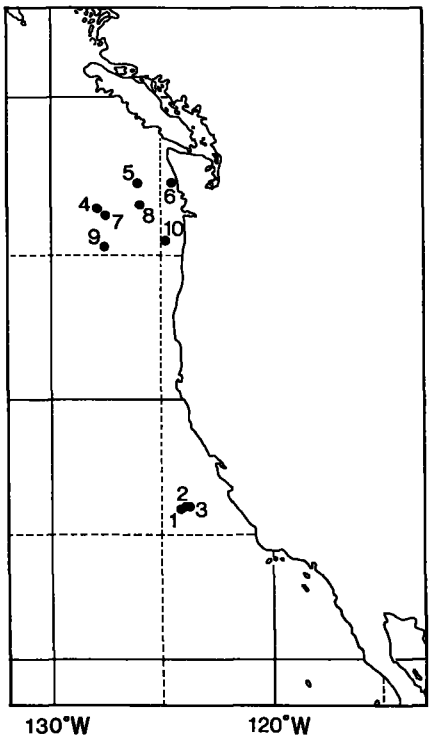
FIGURE 1.—Locations of Pacific saury collection in the North Pacific. Figures by

Sagittae were dissected out from fish and left to dry after removing tissues and membranes. We used a dissecting microscope with a polarizing filter to dissect otoliths from small larvae and juveniles. The otoliths were read either by light microscopy (LM) or by scanning electron microscopy (SEM). Otoliths that were to be read by LM were mounted in EUKITT[5] after dissection. Otolith radius was measured from the focus to posterior margin and the increments were counted along the same transect using the otolith reading system, which was developed by the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, and which consists of a light microscope, a video monitor, a micro-computer, and a digitizer (Methot 1981).

For SEM, otoliths were mounted in epoxy or methacrylate resin. The otolith radius was measured from the focus to the posterior margin with an optical comparator. The otoliths were ground oblique to the sagittal plane parallel to the long axis of the otolith in order to have a flat plane through the otolith nucleus. The polished surface was washed in xylene, using an ultrasonic washer, then dried and etched for 50 seconds with 0.2M EDTA-2Na (disodium ethylenediaminetetraacetic acid). The etched surface was coated with palladium platinum and observed under an SEM (JSM-25) at 15 kV.

The three authors of this paper read saury otoliths independently: the senior author read fish from the western Pacific up to 85 mm by LM, the second author read otoliths from the eastern Pacific by LM, and the third read otoliths from the western Pacific larger than 38 mm by SEM. To confirm that we were all interpreting the same structure as growth rings by SEM and LM, we compared 50 data points read by SEM and 14 points read by LM for western Pacific sauries between 38 and 85 mm. The distribution of increment number versus knob length was the same. We also checked for possible biases for the two readers using LM by having each read the same set of otoliths independently.

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



dots indicate sample numbers in Table 1.

RESULTS

The nucleus of a Pacific saury sagitta is approximately 20 μm in diameter and is composed of four to six small dense bodies which appear to be assemblages of calcareous spherules (Fig. 2a). These dense bodies are separated from one another and each is surrounded by a small concentric ring.

We observed the nucleus areas of otoliths from Pacific sauries collected in the western Pacific in 1985 (sample # 15–22) and found that most of them had a distinct ring of about 27 μm in radius. Between the nucleus and this distinct ring, four (or five) indistinct growth rings were detected (Fig. 2b).

We measured knob lengths of 27 larval and juvenile Pacific sauries before freezing and after thawing, and found that the ratio of these two measurements was 0.997. There was virtually no shrinkage by freezing and thawing. Theilacker (1980) found that preservation of larval northern anchovy, *Engraulis mordax*, in 80% alcohol did not cause additional shrinkage of the body after net treatment. Thus, knob lengths after both 80% alcohol preservation and freezing are comparable to each other, and this measurement corresponds to the size after net treatment. Since shrinkage factors by net treatment are not known for the saury, lengths are uncorrected for net shrinkage.

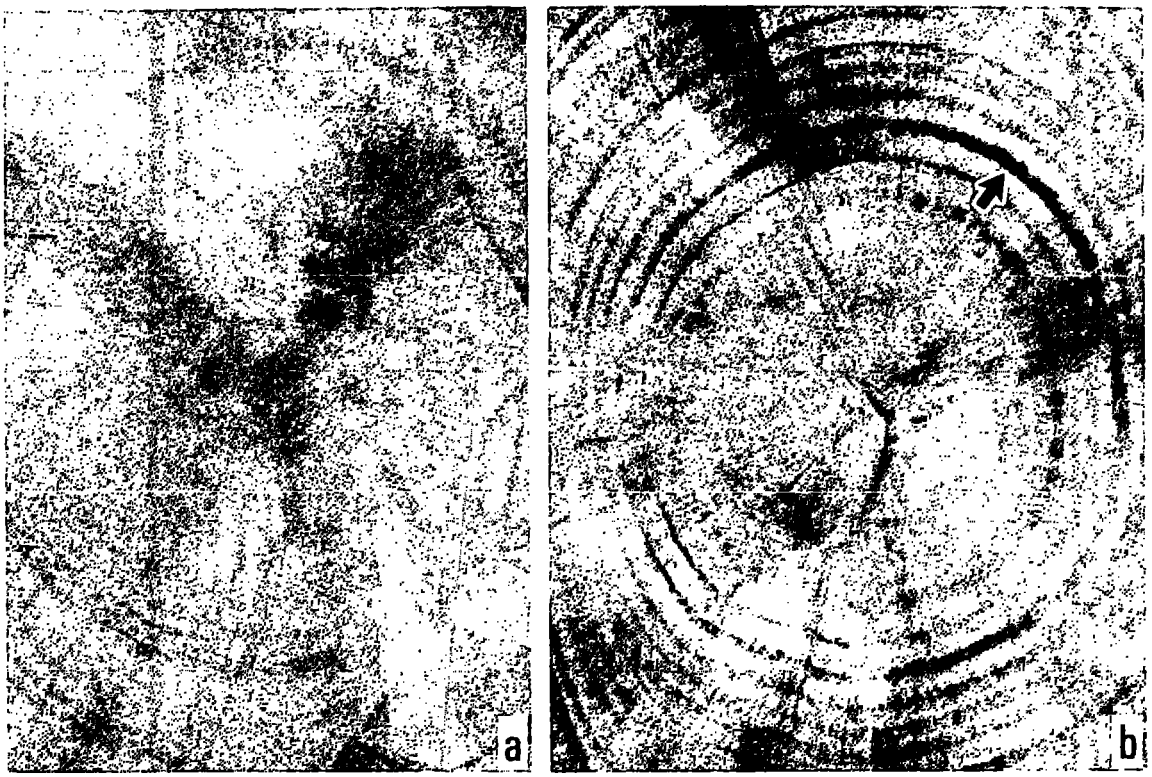


FIGURE 2.—Light micrographs of Pacific saury sagittae. a) Otolith nucleus composed of 5 or 6 separate dense bodies with surrounding cores. b) Assumed 4 embryonic and 1 hatching (arrow) rings.

The daily periodicity of growth increment formation in the Pacific saury has not been verified. For that reason we plotted the number of increments versus knob length instead of age versus length. We used the Laird-Gompertz equation to describe the relations of increment number and length as growth curves for both the eastern and western Pacific saury. Hatching size of artificially fertilized and incubated Pacific saury from the western Pacific was reported to be 7.19 mm in average live total length (Yusa 1960). From the drawing of a newly hatched larva in Yusa's paper, we estimated live knob length to be 6.60 mm. Shrinkage factors of northern anchovy in the size range from 6.00 to 7.99 mm were [illegible] net treatment (Theilacker 1980). Using these values, the capture size of a newly hatched larva of Pacific saury after a 5-min net treatment was estimated to be 5.95 mm and a 10-min treatment to be 5.61 mm. We fixed the hatching size from 5.85 to 5.95 mm in the growth curve, because the Pacific saury larvae at this size are in a more advanced developmental stage and shrank less by net treatment than northern anchovy.

The resulting growth equation for the eastern Pacific saury was

$$KnL = 5.85 \exp((0.0427/0.115)(1 - e^{(-0.0115(I-5))}))$$

and the equation for the western Pacific saury was

$$KnL = 5.95 \exp((0.0504/0.0128)(1 - e^{(-0.0128(I-5))}))$$

where KnL is a knob length in mm and I is the total number of increments observed in an otolith. The [illegible] sumed to have been present at hatching. Data from the western Pacific saury appear to consist of two curves separated around 100 mm in KnL. Two Laird-Gompertz curves fit much better than one curve. The intersection of the two curves was at 114 increments and 100 mm. The growth equation for fish smaller than 100 mm was

$$KnL = 5.90 \exp((0.0865/0.0293)(1 - e^{(-0.0293(I-5))}))$$

and for fish larger than 100 mm *KnL* was

$$KnL = 3.01 \exp((0.0592/0.0126)(1 - e^{(-0.0126(I-5))}))$$

The estimated mean square error, 215.7, of the two curves was smaller than that for a single curve, 351.7. The two-curve model fits much better for the smaller size range up to 100 mm. The estimated mean square error of the two-curve model for this size range, 75.7, was much smaller than that of the one-curve model, 240.8.

The growth rate of Pacific saury in the eastern Pacific was slower than that in the western Pacific (Figs. 3, 4). The knob length of saury in the eastern Pacific would be about 75 mm at 100 rings, 170 mm at 200 rings, and 220 mm at 300 rings, whereas in the western Pacific knob length would be about 100 mm at 100 rings, 230 mm at 200 rings, and 300 mm at 300 rings. Assuming that the rings are formed daily, overall growth rates of the first one year of their life were 0.62 mm/d and 0.85 mm/d for the eastern and western Pacific Ocean, respectively.

The largest specimen examined was 330 mm from the western Pacific, which had 328 increments, and the oldest fish, also from the western Pacific, which measured 320 mm, had only 418 increments. These fish would be classified as very large or large by Novikov's categories of fish size composition (Novikov 1960, 1973). The largest fish examined from the eastern Pacific was 235 mm and had 241 increments. Hughes (1974), however, reported larger fish from the eastern Pacific.

In Pacific saury from the western Pacific, the relation between otolith radius in μm (OR) and knob length in mm (*KnL*) was linear on logarithm-logarithm coordinates (Fig. 5). The equation computed by the geometric mean regression (Ricker 1973) was

$$\ln (OR) = 2.33 + 0.749 \ln (KnL) \quad (r = 0.979).$$

The otolith radius at hatching (5.9 mm *KnL*) calculated by this formula was 38.9 μm, which was 12 μm larger than the radius of the presumed hatching ring.

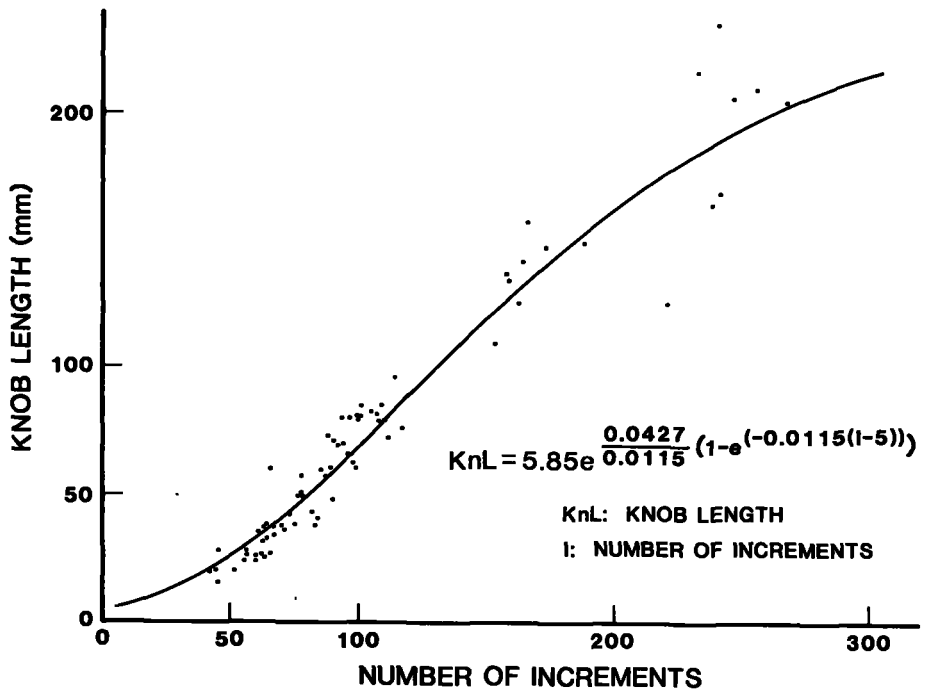


FIGURE 3.—Growth curve of the eastern Pacific saury.

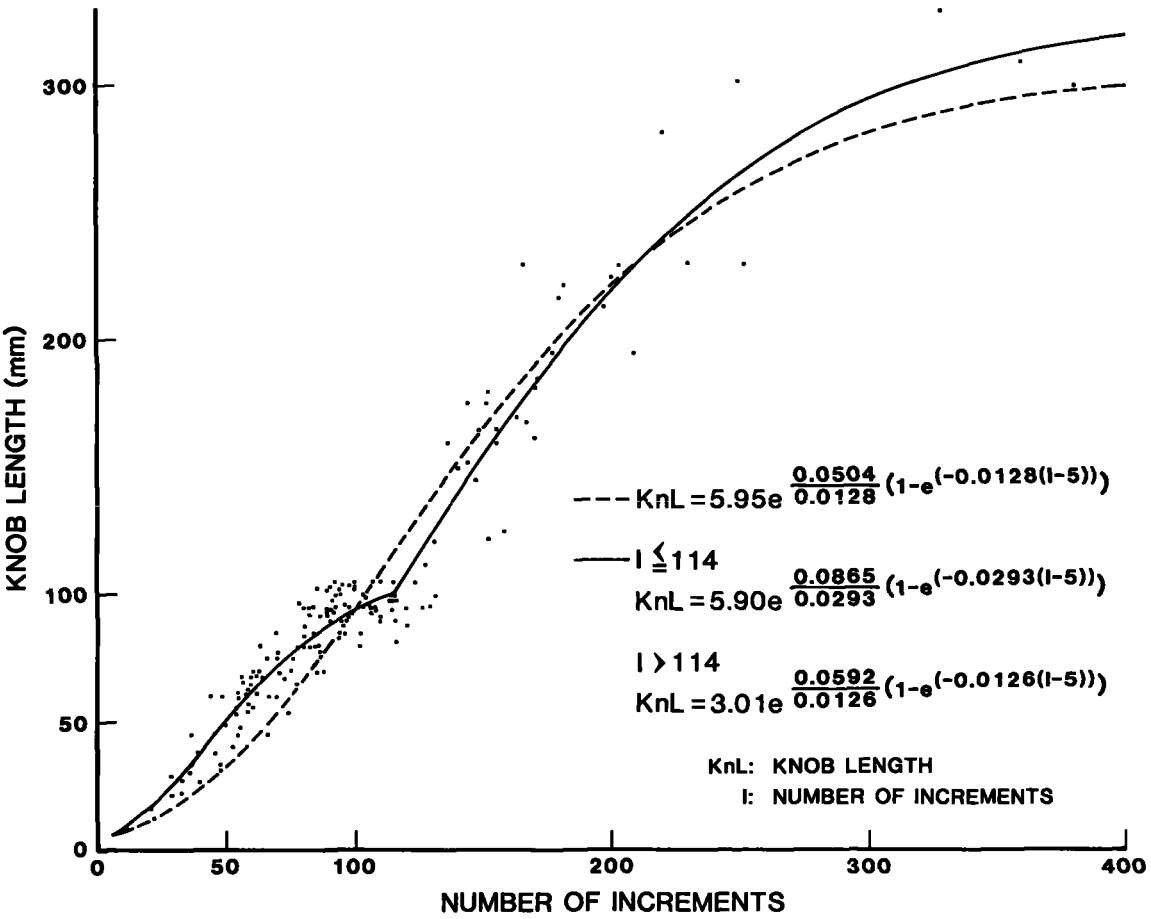


FIGURE 4.—Growth curve of the western Pacific saury.

DISCUSSION

The microstructure of otolith growth increments of the Pacific saury is similar to that of daily increments in some other fishes (Nishimura et al. 1985). Thus, the following discussion is based on the assumption that the increments are daily growth rings. A rearing experiment of larval sauries is under way in the senior author's laboratory to verify daily periodicity of the increment formation.

Formation of a few embryonic growth rings or a lamellar structure has been reported in California grunion, *Leuresthes tenuis*, (Brothers et al. 1976); mummichog, *Fundulus heteroclitus*, (Radtke and Dean 1982); and walleye pollock, *Theragra chalcogramma*, (Nishimura and Yamada 1984). Radtke and Dean (1982) mentioned that deposition of growth rings in the embryonic stage might be related to a long incubation period. Pacific saury has a long incubation period—about 17 days under 13.5°–15.7°C (Yusa 1960). At this temperature, eye pigmentation begins 7 or 8 days before hatching, and pectoral fins show constant movement from 5 or 6 days before hatching (Yusa 1960). Notochord flexion occurs about midway through embryonic development at 14°–22°C (Uchida et al. 1958). Thus saury is more advanced at hatching than killifish based on the embryonic development of killifish reported by Armstrong and Child (1965). Observing the central area of otoliths, we found four faint rings and a dark ring immediately outside of those rings. We assumed therefore that the four faint rings are embryonic rings and the dark ring is the hatching ring. This assumption may be confirmed by examining otoliths of late embryos and newly hatched larvae of saury.

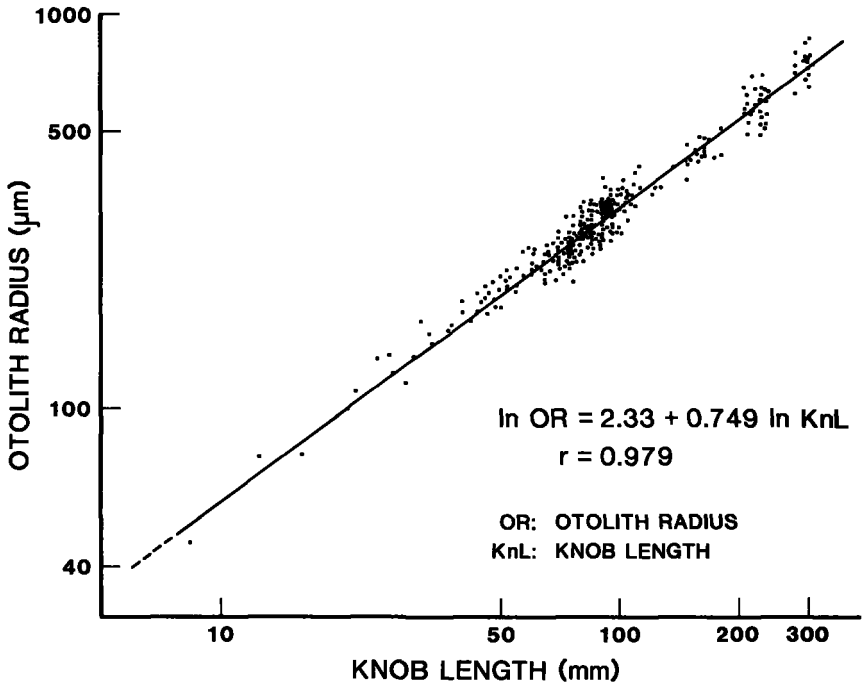


FIGURE 5.—Knob length and otolith radius relationship of the western Pacific saury.

Previous studies on age and growth of the Pacific saury have based on annuli on scales and/or otoliths. Sunada (1974) found five age groups in Pacific sauries off southern Oregon, California, and Baja California. Mean fork lengths of age groups were 171, 220, 246, 270, and 268 mm for age 0, 1, 2, 3, and 4, respectively. Hughes (1974) examined age composition of 5,248 sauries collected in waters off California up to Vancouver Island. He found spring- and autumn-born fish in his samples, but little difference was noted in growth rates between two groups. Approximate knob lengths of 1.0- to 5.0-year-old fish were 180, 230, 255, 290, 310 mm. The growth rates given in these two papers are not very much different. The saury grows at 0.5–0.6 mm/d up to 1 year old, which is almost equal to our growth rate in the eastern Pacific, 0.62 mm/d. Hatanaka (1955) found five age groups in the western population of the saury, 0–4 years old, and estimated mean body length of age groups to be 80, 160, 230, 265 mm for 1- to 4-year-old fish, respectively. Novikov (1960, 1973) divided sauries captured in autumn into five size groups, very small (– 200 mm), small (201–240), medium (241–290), large (291–320), and very large (321+), and assigned the small, medium, and large to 1-, 2-, and 3-year-old with maximum 5-year-old fish.

A different model of Pacific saury growth in the western Pacific was proposed by Hotta (1960) based upon a hypothesis of two subpopulations. He separated the saury into spring-spawning and autumn-spawning populations based upon the observations of fish size composition, scales, otoliths, and numbers of vertebrae. He assigned four ages of half year intervals, 1.0, 1.5, 2.0, 2.5 years old, to fish 210–240, 260–280, 290–300, and 310–330 mm, respectively. The growth rate up to 1 year was 0.6–0.7 mm/d. Kim and Park (1981) examined Pacific sauries from Korean waters and found four size groups of four different ages of half-year intervals as well. They presented two growth models for each of two subpopulations, spring and autumn spawning, based upon the von Bertalanffy equation. The sizes at ages were almost identical to those of Hotta (1960). However, the hypothesis of two saury subpopulations in the western Pacific is not supported by electrophoretic analyses of genetic separation (Numachi 1971; Hara et al. 1982).

The average growth rate of the western Pacific saury in this paper was 1.1 mm/d from 0 to 8 or

9 months old. It was still faster than Novikov's growth rate of the corresponding age period (0.83 mm/d), which was the highest rate of all the previous reports. The fish would become 316 mm in one year according to our model.

Support for the fast growth rate of Pacific saury presented in this paper in the western Pacific can be found in rearing experiments. Hotta (1958) reared young sauries caught by a set net. He reared them in a crawl and fed them minced anchovy and mackerel twice a day. Young sauries 116 mm in mean length became 172 mm in the rearing period after 72 days. The growth rate was 0.78 mm/d. The sauries fed three times a day grew 130–143% faster than the group fed twice a day. Thus growth rates of young sauries may be higher than 1.1 mm/d (0.78 × 1.4 mm/d) when food is readily available. Our growth rate of sauries in this size range was approximately 1.5 mm/d in the western Pacific. For Atlantic saury, *Scomberesox saurus scombroides*, reared by Brownell (1983), the average growth rate of the larvae was 0.62 mm/d from hatching (7.5 mm SL) to 47-day old (36.8 mm SL). The growth rates of *Cololabis saira* in a corresponding period were 0.48 mm/d in the eastern Pacific and 1.0 mm/d in the western Pacific.

Our results indicate that the growth rate of Pacific saury in the western Pacific is much higher than in the eastern Pacific. This could be due to a difference in food availability between the two areas. However, mean zooplankton standing stock in 1951–66 was 34.8 g/m^2 in the California Current region in June (Smith and Eppley 1982), whereas that of Kuroshio water off southern Japan was 4.7 g/m^2 and of Oyashio area off northern Japan was 25.7 g/m^2 in May to July (Odate 1986). Thus, differences in zooplankton standing stock do not explain the difference in growth rates.

On the other hand, there seems to be a reasonable explanation for the reacceleration of growth rate at around 100 mm in the western Pacific saury. The western sauries hatch out mainly in offshore water of the Kuroshio Current (lat. 31–33°N) off Japan in winter. They migrate north to the Oyashio area (up to 46–50°N) where copepods are highly available. Young and adult sauries feed actively and gain fat. They are in the northward migration stage in early summer when they are about 100 mm, and are moving from poor Kuroshio water to rich Oyashio water (Fukushima 1979). High zooplankton standing stock in the Oyashio water and its derivatives might be responsible for the reacceleration of growth rate in fish older than 100 days.

The growth rates of Pacific saury in the western Pacific may differ from year-to-year due to environmental factors and may result in changes in size composition of the fish. Between 1968 and 1972, mean knob length of exploited sauries in the western Pacific was 170-250 mm, whereas in the 1980's the major mode in the size composition was 290-310 mm (S. Kosaka[6]). This increase could have been due to an acceleration of growth rate or a shift of spawning season to early months or both in recent years. The high growth rate of western Pacific saury presented in this paper has come from specimens collected in 1984 and 1985. The growth rate in the late 1960's and early 1970's may have been lower than that presented in this paper. Investigation of the interannual variation in growth rates using daily increments would distinguish between these two hypotheses.

We used three different gears to collect Pacific saury samples in the western Pacific. Knob lengths of sauries collected were from 8.3 to 125 mm by ring net, 145 to 282 mm by gill net, and 300 to 330 mm by stick-held dip net. Sauries of 125–145 mm might not be available either to the ring net or to the gill net. Further, the ring net may select small juveniles of a cohort in the size range over 100 mm, and this may have produced the two growth curves. This problem needs to be examined further with data on gear selectivity.

We do not know how long Pacific sauries survive after becoming adult. The oldest specimen in our sample was about 14 months old after hatching (418 increments). The largest saury aged (330 mm), which had 328 growth rings, is close to the maximum size. Although the maximum known length of the Pacific saury was reported to be about 400 mm (Hubbs and Wisner 1980), the largest fish exploited in Japan is about 340 mm. Therefore, the lifespan of the Pacific saury is about one year in the western Pacific. Our results are more consistent with those of Kosaka (1979) who found two age groups (0 and 1 year) than those (Sablin 1979) who found three age groups (0, 1, and 2 years).

In Japan, fishing efforts of the Pacific saury is regulated by fishing season as well as by the number of fishing boats. The fishing season starts in mid-August. Pacific sauries hatched in the main spawning season are about 250 days old at this time of year (approximately 270 mm) and are growing at the rate of 0.8 mm/d. Thus a 2-wk postponement at the beginning of fishing season would result in an 11 mm (10–15 g body weight) increase of average fish

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length. The biomass and yield of Pacific saury need to be reestimated based on faster growth rates presented here.

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OTOLITH ULTRASTRUCTURE OF SMOOTH OREO, *PSEUDOCYTTUS MACULATUS*, AND BLACK OREO, *ALLOCYTTUS* SP., SPECIES

N. M. DAVIES,[1] R. W. GAULDIE,[1,2] S. A. CRANE,[1] AND R. K. THOMPSON[3]

ABSTRACT

The ultrastructure of sagittal otoliths from 14 *Pseudocyttus maculatus* and 25 *Allocyttus* sp. individuals were examined to determine their suitability for estimating age in these two species. Scanning electron microscopy revealed high levels of complexity in both external surface topography and internal structural organization in the sagittae of both species. Many different crystal forms were found, including calcite-like prisms. A close similarity in otolith structure exists between the two species. Deposition of check rings analagous to annual and daily growth increments was found to be irregular with the underlying complexity of crystalline growth obscuring the finer (analogous to daily) growth rings, making their periodicity difficult to validate and implying that with present techniques the sagittal otoliths of the oreo species *Pseudocyttus maculatus* and *Allocyttus* sp. are not suitable for age estimation.

The smooth oreo, *Pseudocyttus maculatus*, and the black oreo, *Allocyttus* sp., are two related species of the family Oreosomatidae. They are both important commercial species in New Zealand. The black oreo is the most commonly caught oreo in New Zealand waters, while the smooth oreo is the second-most commonly caught oreo. Little is known about the biology of these fish. The black oreo is endemic to New Zealand while the smooth oreo occurs in New Zealand, South Australian, South African, and South American waters (Last et al. 1983). In the waters south of New Zealand, the distributions of the two species overlap (McMillan 1985). The habitat range of the smooth oreo is between 650 and 1,200 m, and that of the black oreo is between 600 and 1,200 m (McMillan 1985).

A preliminary examination of the ultrastructure of otoliths [sagittae] of these fish was undertaken as part of a study to establish an ultrastructural basis for a suitable ageing technique. This study describes the external and internal structure and organization of the otoliths in terms of the suitability of the various check rings of the sagittae for age estimation.

MATERIALS AND METHODS

Three otoliths (the sagitta, astericus, and lapillus) are contained in the endolymphatic sac (Fig. 1a). The sagitta is the largest otolith and is located in the most ventral position in the sac. The arrangement of the three otoliths in the endolymphatic sac ranges between the primitive where a large astericus and sagitta with no lapillus is present (Gauldie et al. 1986) and the typical teleost arrangement where a small astericus is located close to the sagitta, and an even smaller lapillus is displaced into the atrium of the semi-circular canal. The oreosomatids are primitive fishes taxonomically, lying in the order Beryciformes (Nelson 1976), and the arrangement of otoliths reflects the taxonomic position of the fish. The orientation of otoliths described here refers to the orientation in situ. The lateral face is the outward (antisulcal) surface; the medial face is the inward (sulcal) surface. Investigation was restricted to the sagitta primarily because of the difficulties in establishing homologies for daily and annual type check rings in the astericus and lapillus.

Sagittae were dissected from 14 smooth and 25 black oreo individuals caught in bottom trawls off the east coast of New Zealand. These individuals ranged in length from 24.5 to 40.1 cm (black oreo) and 35.1 to 51.2 cm (smooth oreo).

Whole otoliths were photographed at 6× to 20× using a WILD[4] photomicroscope. The sagittae were embedded on glass slides in epoxy resin with the antisulcus surface uppermost and finely ground on a Struers Planapol-2 petrographic grinder. The

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

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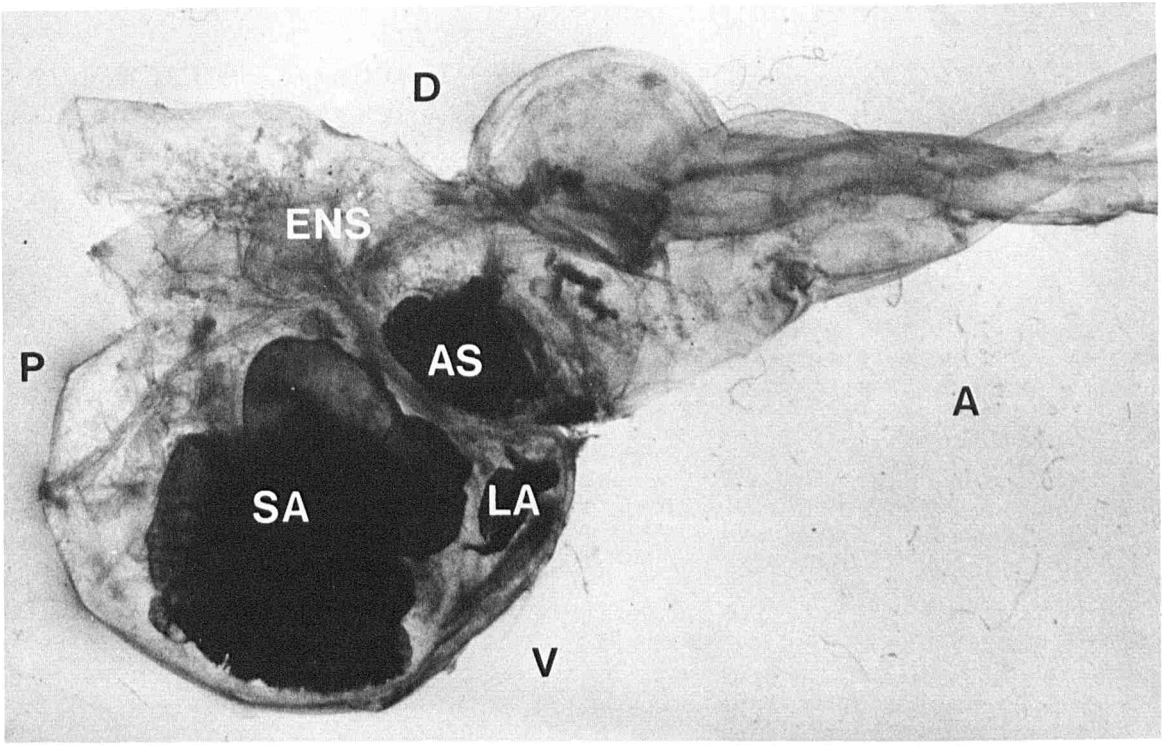

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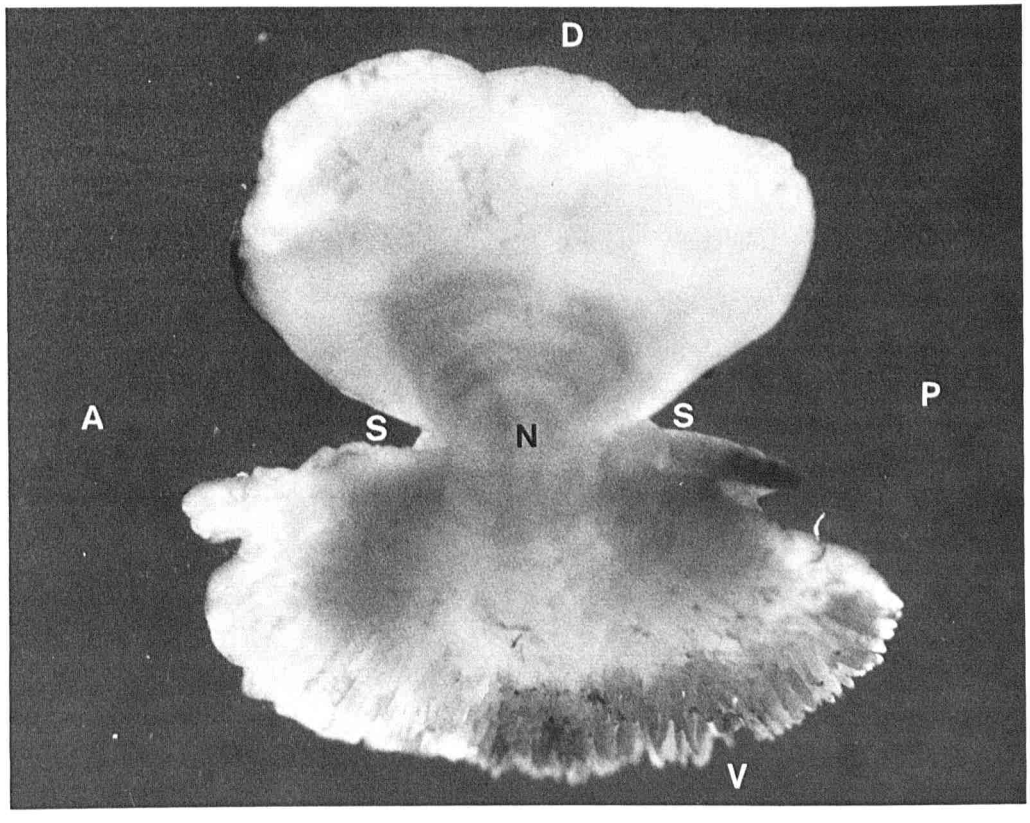

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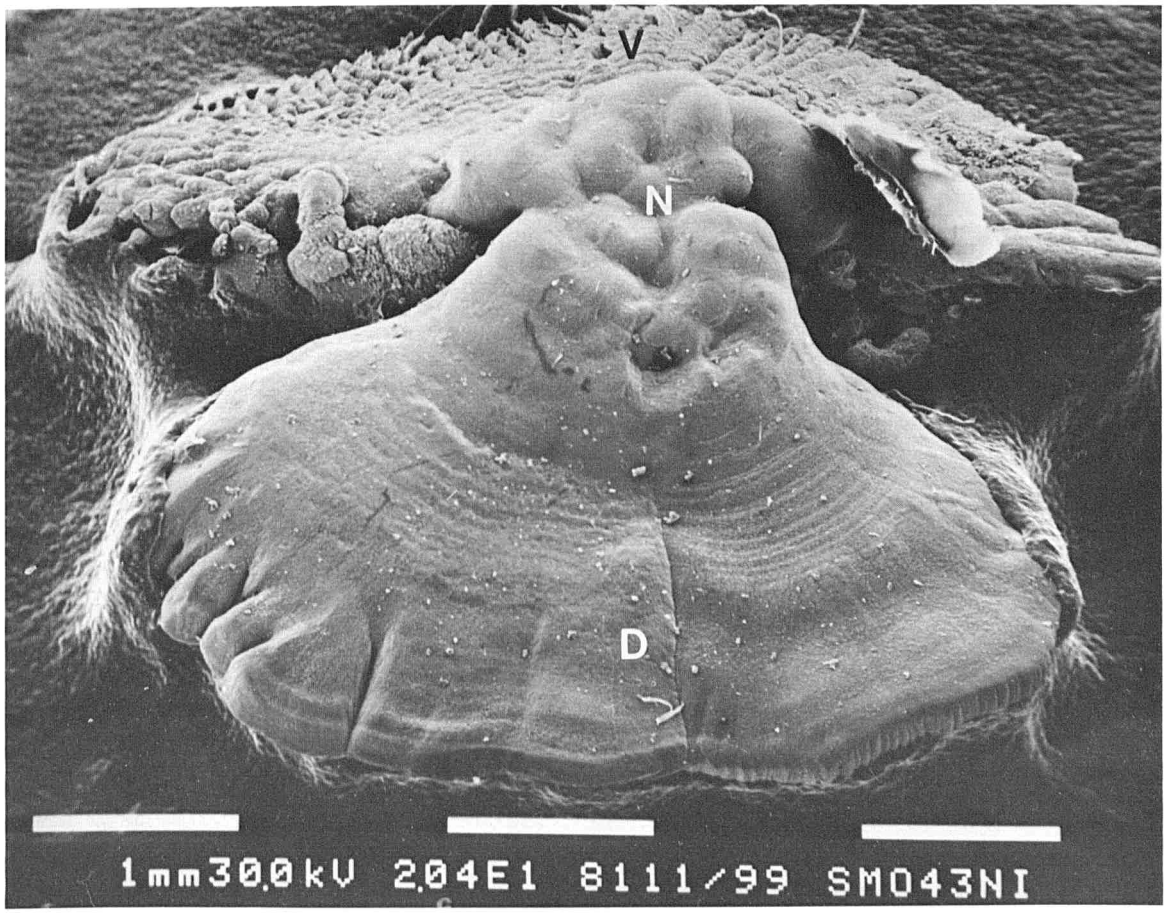


FIGURE 1a.—Relative positions of the otoliths in the right endolymphatic sac (ENS) of the smooth oreo in lateral view: astericus (AS), lapillus (LA), and sagitta (SA). Anterior (A), dorsal (D), posterior (P), and ventral (V) surfaces are indicated. Magnification = 6.3×.

b.—Dorsal (regular) and ventral (irregular) lobes of the otolith in lateral view, nucleus (N), sulcus (S), and rest as in Figure 1a. Magnification = 12.5×.

c.—SEM of the lateral surface topography of the otolith. Scale bar = 1 mm.

ground surface was polished with 2000 grit wet and dry paper to yield a smooth surface for etching. The most successful results were obtained by etching with a 0.1 M solution of disodium salt of EDTA. The otoliths were immersed in this solution for 15 to 20 minutes. Other suitable etching solutions employed were 1) a 1% solution of HCl for 20 to 30 seconds and 2) a 2% solution of Histolab RDO (a commercial etching solution comprising a mixture of HCl and EDTA) for 5 minutes. A cellulose acetate peel was made of the etched surface to obtain an exact replica of the surface features. The peel was placed on a microscope slide under a cover slip, cleared with ethanol or distilled water, viewed, and photographed using a Zeiss photomicroscope. Direct observations of thin sections (about 20 μm) of otoliths did not show any more information than that observed in acetate peels. Acetate peels had the advantage of allowing successive grinds to be examined thereby avoiding the problem of losing information that might be located only in very narrow layers within the otolith.

Scanning electron microscope (SEM) photographs were taken of otoliths using a Phillips 505 SEM. Whole otoliths were glued on to SEM pin type mounts, cemented in position with contact cement, and sputter-coated with gold at approximately 5 Torr. The external surface topography of both the medial and lateral faces of the otoliths was photographed. Selected pieces of otoliths broken by thumb

pressure were examined and photographed to obtain internal structural information. Finely ground cross-section surfaces were also polished and etched for examination with the SEM.

RESULTS

Smooth Oreo Otolith

The sagitta is clearly divided into two distinct structures: a small, smooth, regular dorsal lobe and a larger, irregular ventral lobe (Fig. 1b). The irregular lobe has branched crystal formations and clefts at the ventral edge. The lateral face topography is complex (Fig. 1c). The central bumpy area contains the nucleus between the two lobes. Radiating outwards from the nucleus are concentric ridges on the antisulcul surface.

The crystal morphology of the lateral surface of the sagitta is variable. Over much of the central parts of the sagitta, large and variably oriented crystals give a coarse appearance to the surface of the otolith (Fig. 2a) which presumably obstructs, by diffraction, potentially clear zones in the whole otolith viewed by transmitted light. At the edge of the regular lobe, the crystal type alters to form slabs of crystal layers (Fig. 2b). The analogous area on the irregular lobe yields variable crystalline structures with complex alignments (Fig. 2c). Deep troughs and branching furrows break up the crystal forms at the edge of the irregular lobe.

The medial surface has three distinct parts: the central sulcal area, the edge of the irregular lobe, and the edge of the regular lobe (Fig. 3a). Raised ridges and two prominent knobs are found in the central sulcal area. Crystals compacted into a petal-like growth pattern are found in this part of the otolith (Fig. 3b). Contrasting to this, more porous crystal structures occur in the edge areas of the regular lobe (Fig. 3c). Further variety is found on the irregular lobe, where a very porous, honeycomb-like crystal arrangement exists (Fig. 3d). At the

a

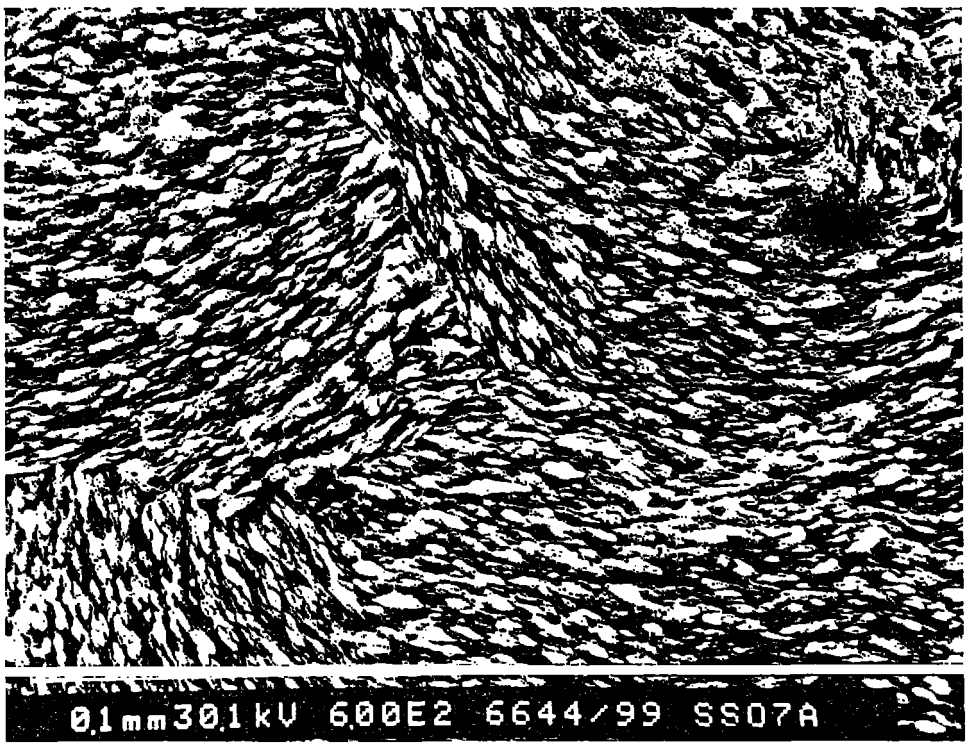
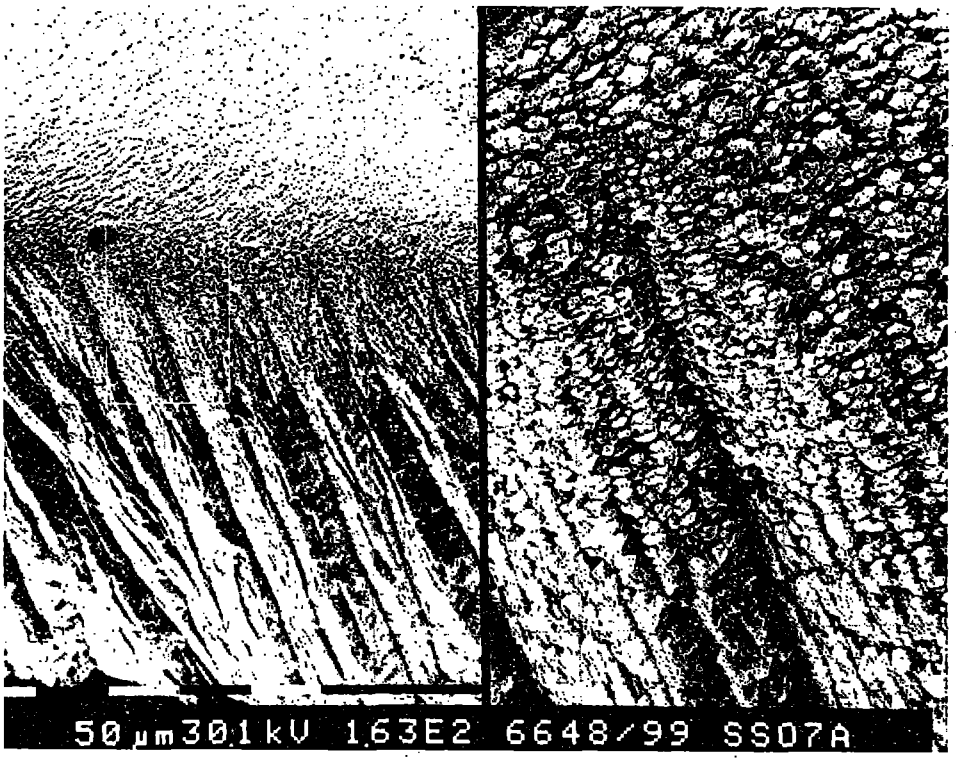


FIGURE 2a.—Coarse crystal structure of the central lateral surface of the smooth oreo otolith. Scale bar = 0.1 mm.

b.—Split-screen SEM of the transition of the crystal-type at the edge of the lateral surface of the regular lobe. Magnification = 163× and 652×.

c.—Haphazard crystal alignments at the edge of the lateral face of the irregular lobe. Scale bar = 0.1 mm.

b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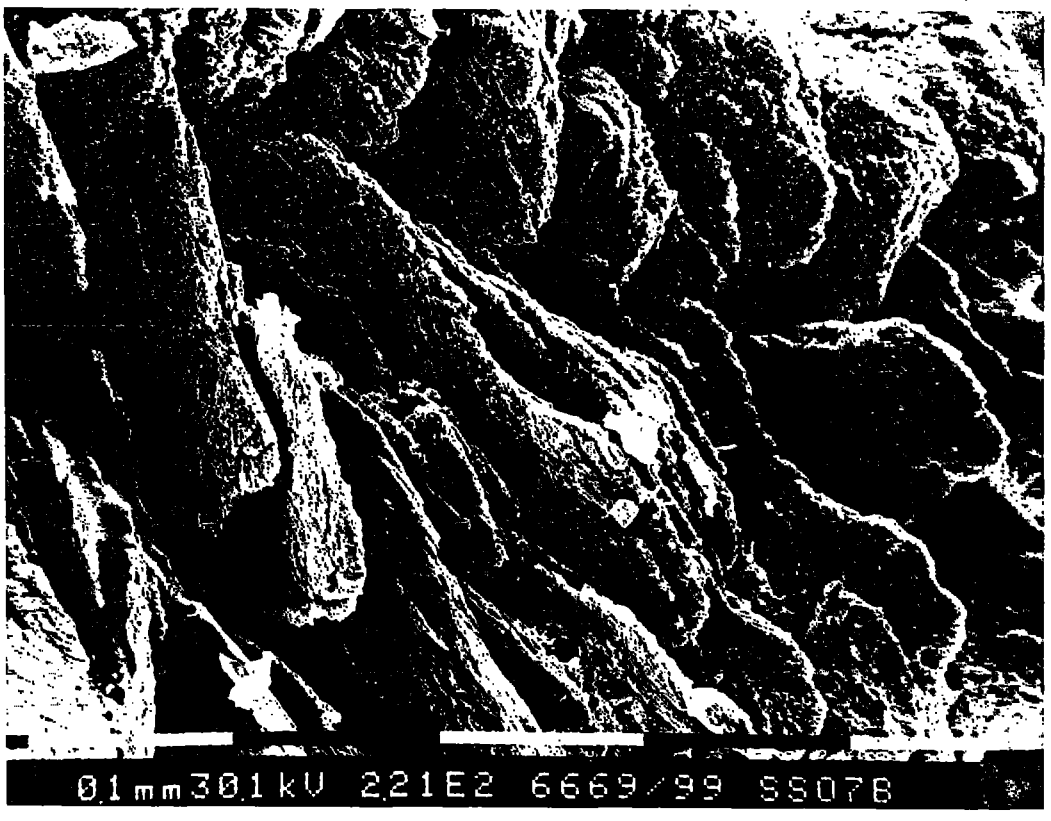
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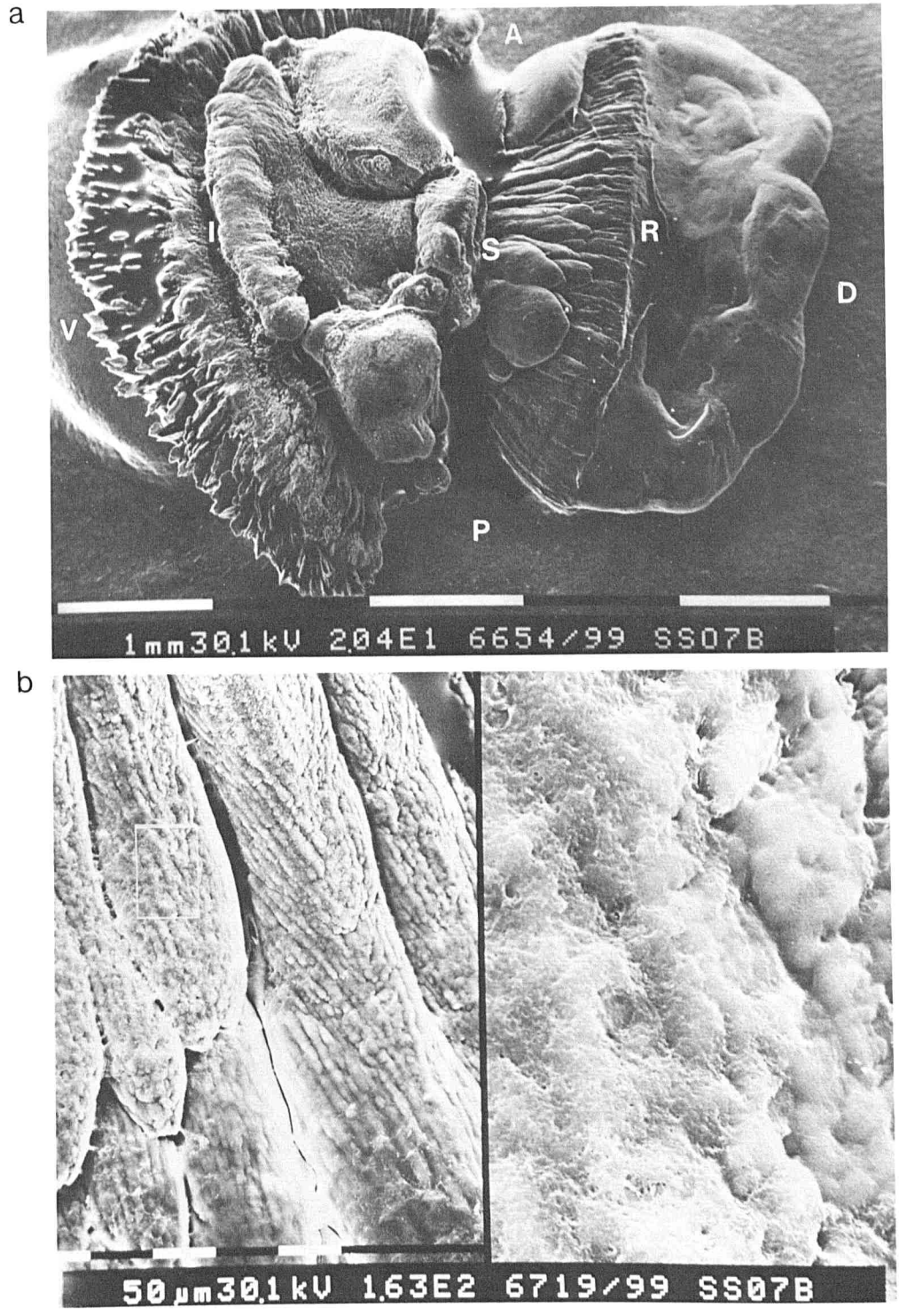

FIGURE 3a.—Medial view of the smooth oreo otolith showing the irregular lobe (I), regular lobe (R), and sulcus (S). Scale bar = 1 mm.

b.—Split-screen SEM of petallike crystal growth in the sulcus on the medial surface. Magnification = 163× and 1141×.

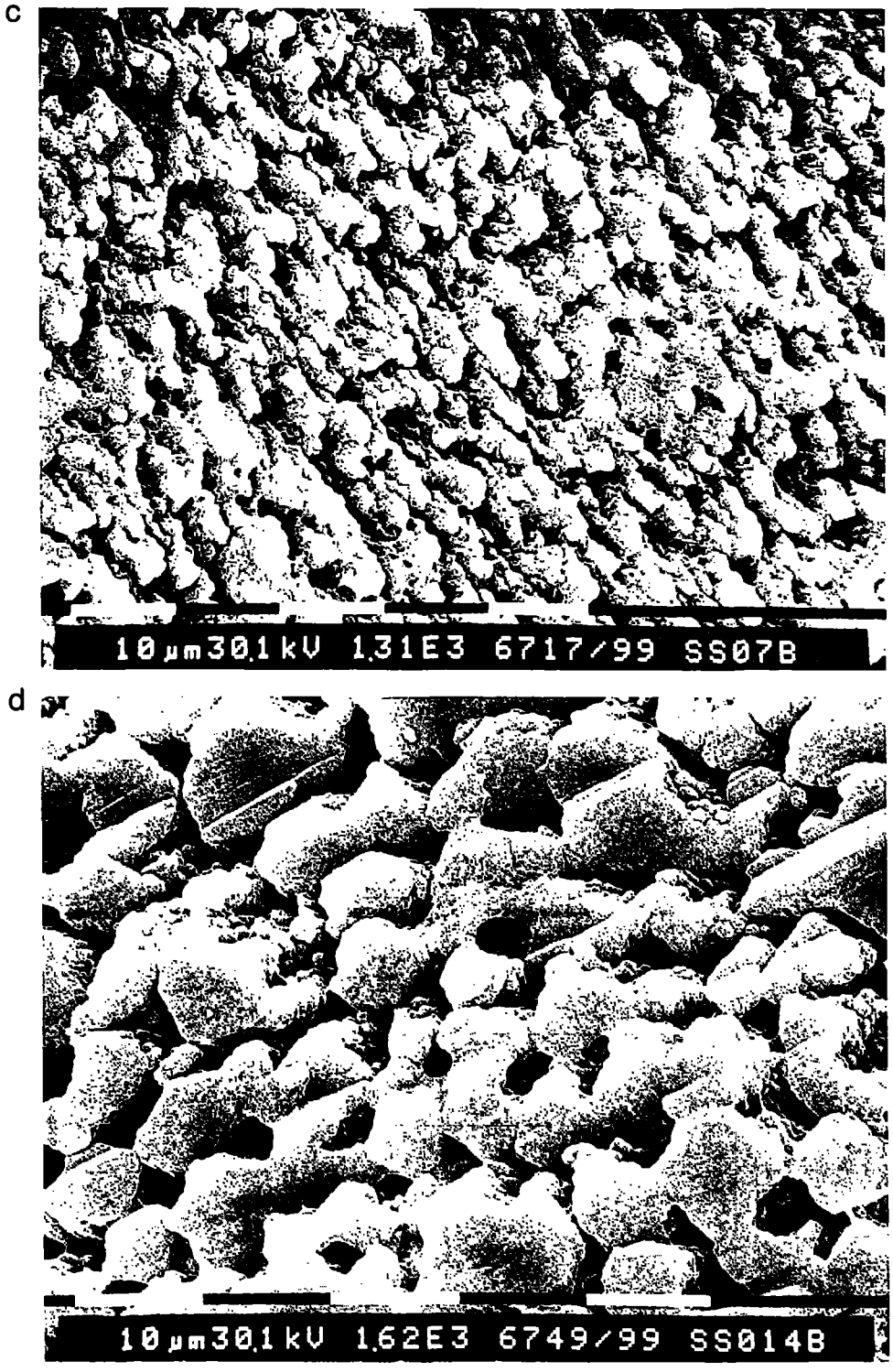

FIGURE 3c.—Porous crystals on the medial surface of the regular lobe. Scale bar = 10 µm.

d.—Honeycomblike crystal structure on the medial surface of the irregular lobe. Scale bar = 10 µm.

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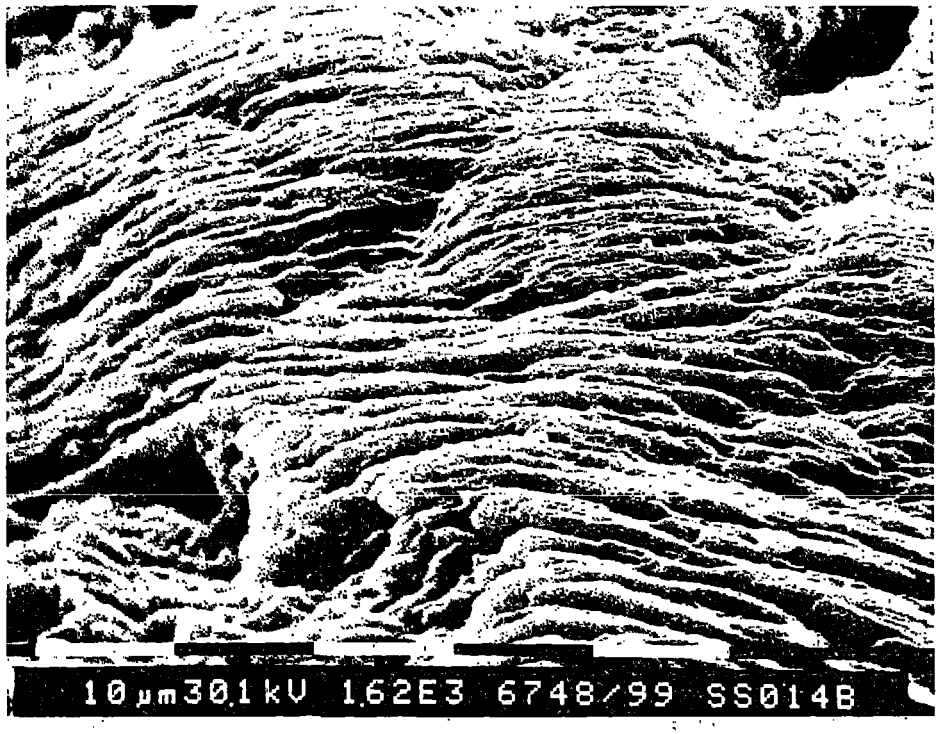


FIGURE 3e.—A laminar pattern of crystalline growth on the medial face of the irregular lobe. Scale bar = 10 µm.

edge of this lobe, a laminar crystalline growth pattern develops, adding to the overall variation of crystal structures on the medial surface (Fig. 3e). Other studies of otolith ultrastructure present the otolith as homogeneous in crystal form, composed almost entirely of monoclinal aragonite crystals (Degens et al. 1969). The complex crystallinity of the oreo otoliths resembles that of the mollusc shell, which, although aragonitic, often has a pattern of complex variation in crystal habit (Carriker et al. 1980).

Within the broken otolith, the nucleus lies at the center of a spherical primordium (Fig. 4a). Crystals grow outwards from the primordium and epitaxial (Degens 1976) growth patterns exist (Fig. 4b). Complex leaf-shaped crystals occur in areas directly beneath the lateral surface of the fractured irregular lobe (Fig. 4c). Beneath the medial surface, a remarkable series of hexogonal crystals of calcite occur as large rectangular blocks embedded *within* the otolith (Fig. 4d). Calcitic prisms have been described in molluscs as resulting from the regeneration of broken shells (Watabe 1983). It is difficult to imagine otoliths being broken and regenerated in situ.

Major and minor check rings similar to those described (Gauldie 1987) for otoliths from the orange roughy, a deepwater species from the same habitat, occur (Fig. 4e). When polished and etched, the check rings become clearly visible with deep etched checks occurring between the less deeply etched checks analagous to microscopic growth increments in other species (Fig. 4f). At a higher magnification the finer increments become obscured by the coarseness of the underlying crystal type (Fig. 4g). Those fine increments that are visible occur irregularly and have varying widths.

Large-scale rings analogous to opaque/hyaline annual zones were observed in the regular lobe. The mean width of these zones, measured using transmitted light (Fig. 1b), was 0.34 mm (±0.06). The concentric ridges observed by SEM on the lateral surface of the regular lobe (Fig. 1c) have a mean width of 0.37 mm (±0.06). These two structures, opaque/hyaline zones and surface ridges, have about the same width with no statistically significant differences between them.

Examination of otolith cross sections reveals widely spaced, large rings with many finer rings in between (Fig. 4h). When examined in greater detail, the demarcation between the large and finer rings

a

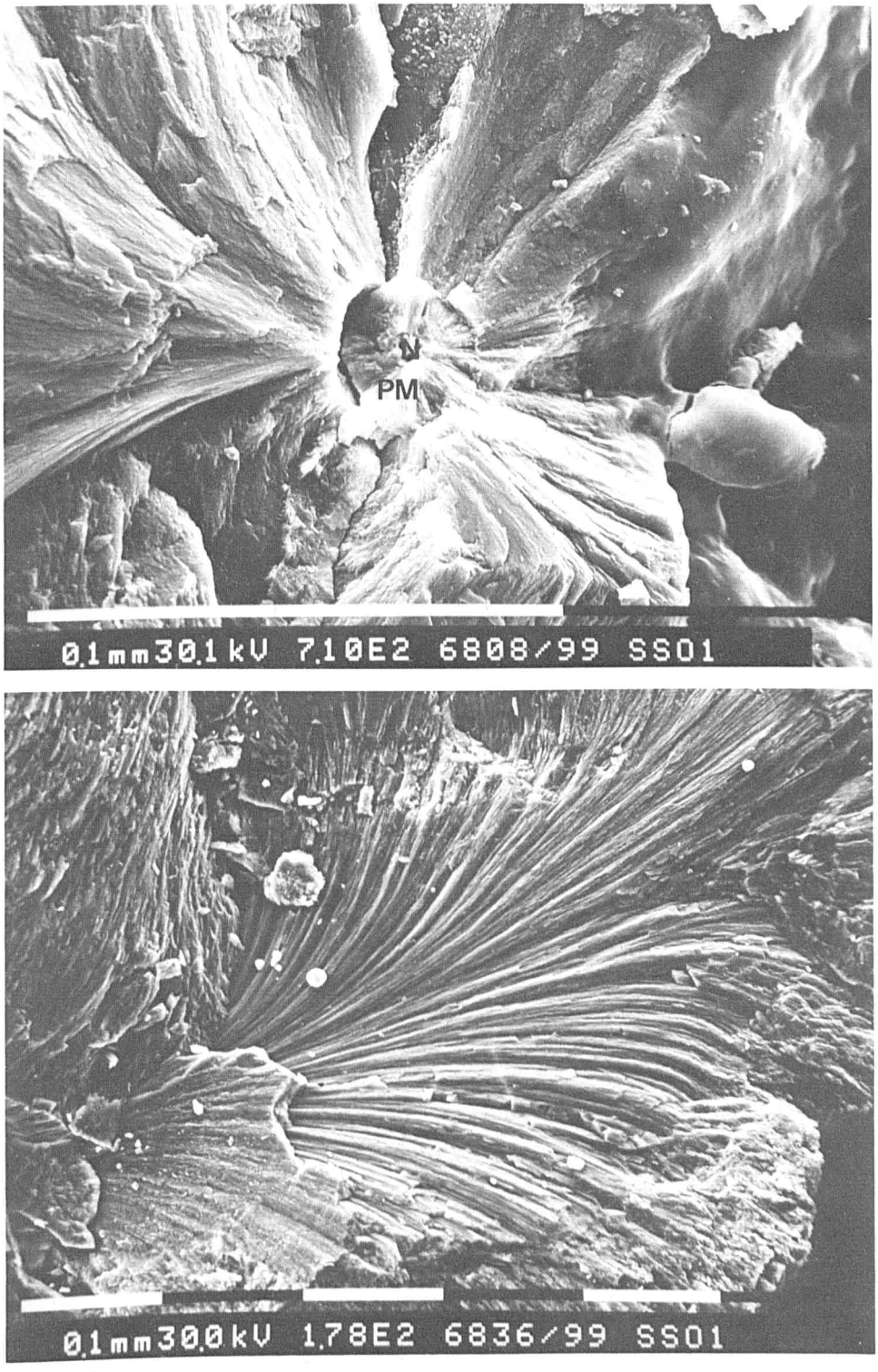
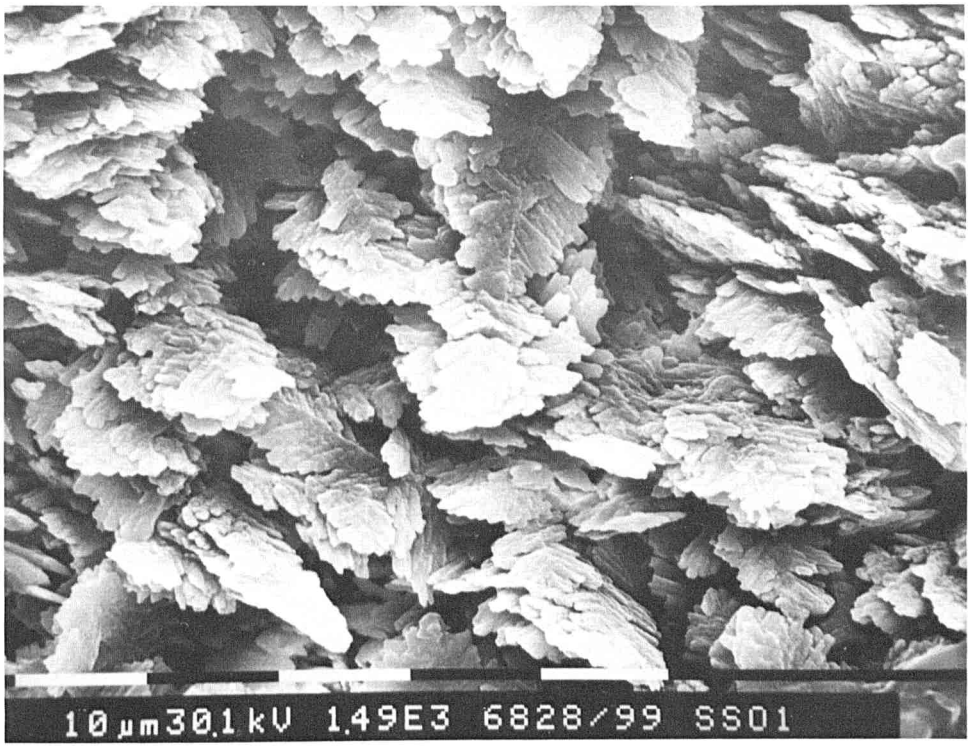


FIGURE 4a.—Broken smooth oreo otolith reveals the spherical primordium (PM) and nucleus (N) and the surrounding radial crystal growth. Scale bar = 0.1 mm.

b.—Epitaxial crystal development in the broken otolith. Scale bar = 0.1 mm.

c



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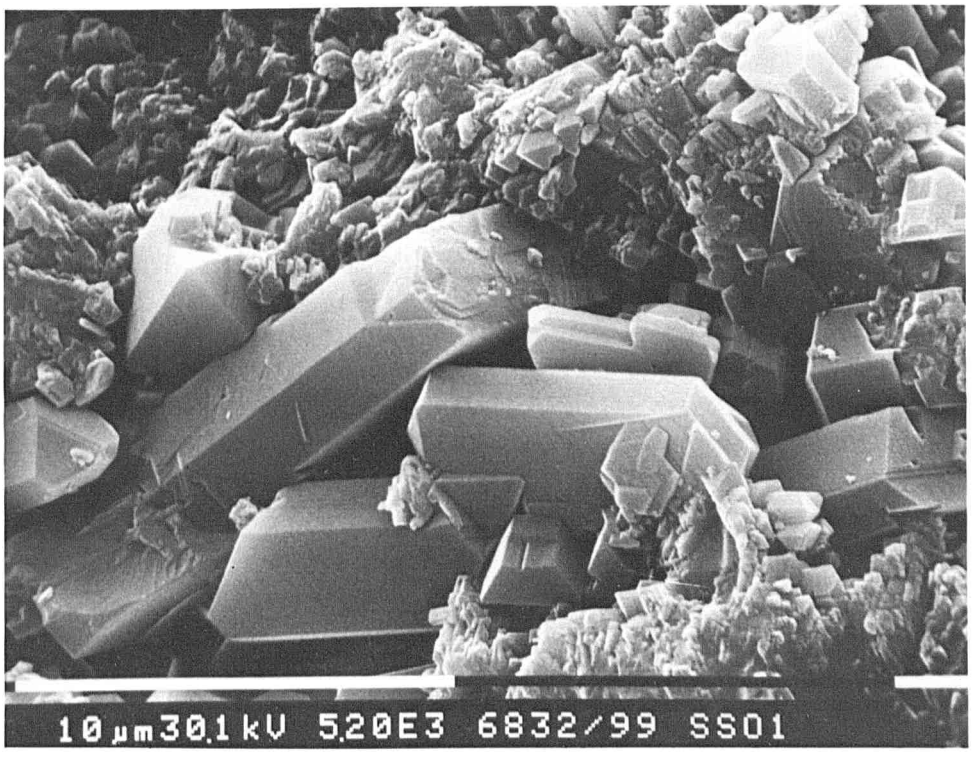
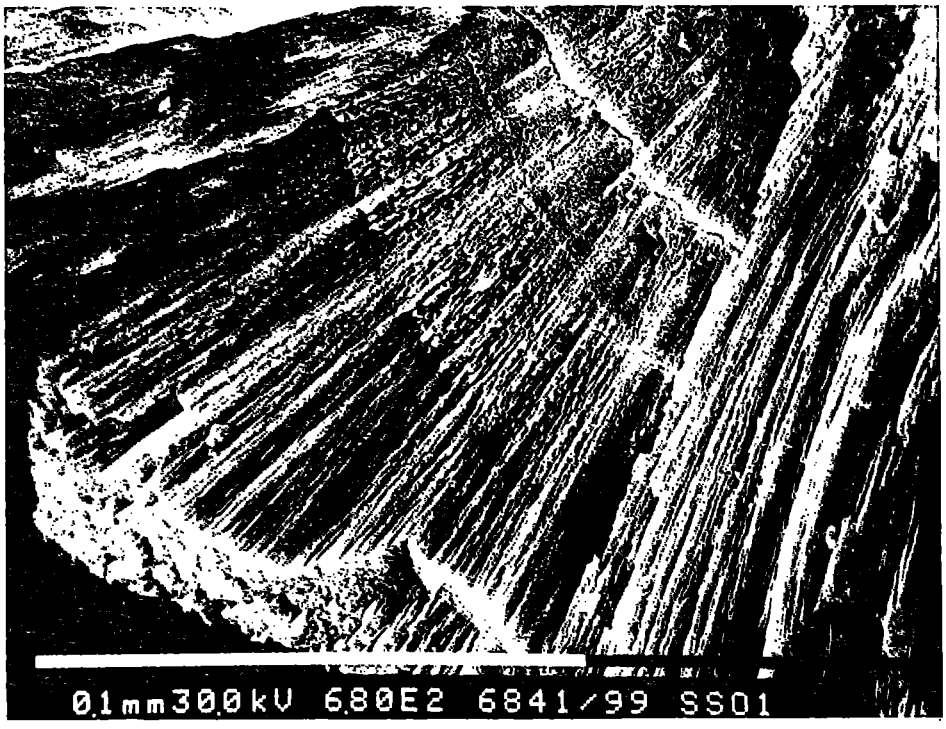


FIGURE 4c.—Leaf-shaped crystals beneath the lateral surface of the broken otolith. Scale bar = 10 µm.
d.—Calcitic prism crystals beneath the medial surface of the broken irregular lobe. Scale bar = 10µ.

e



f

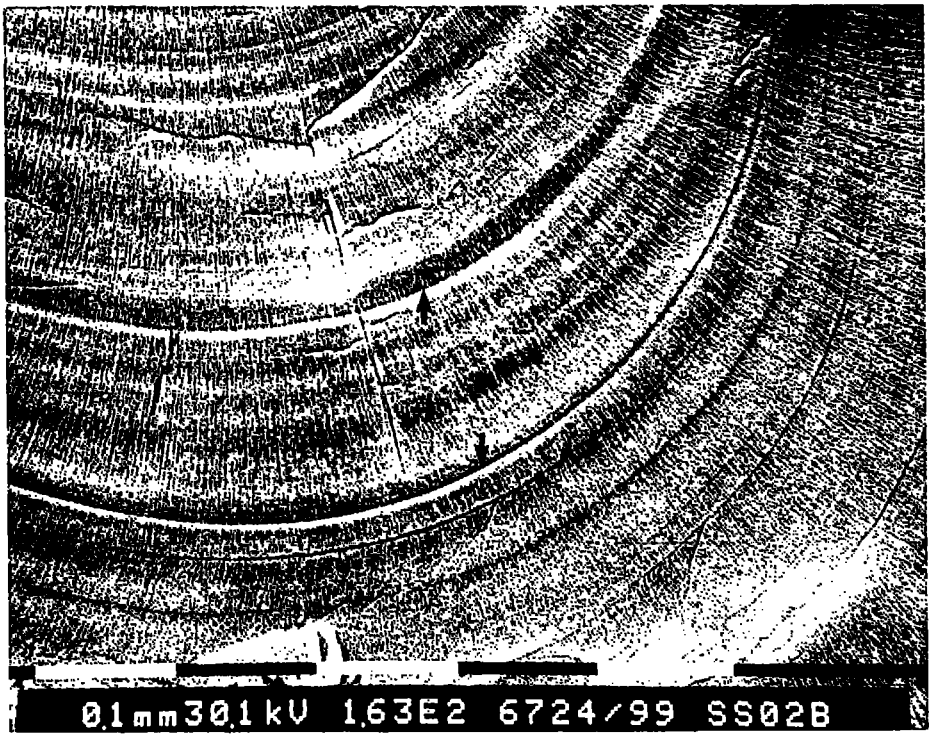
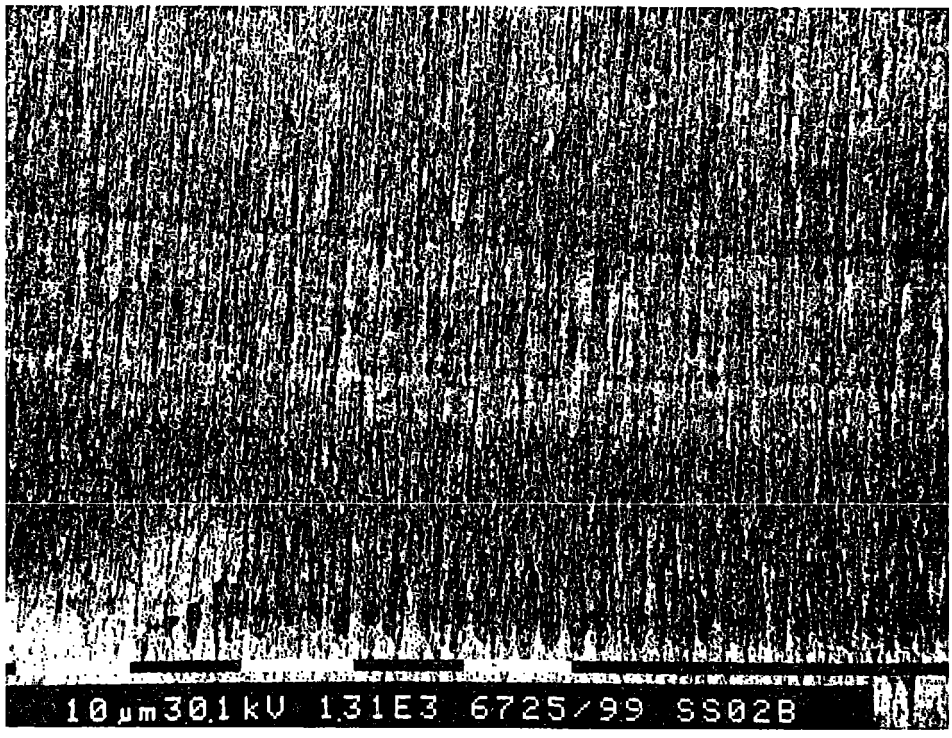


FIGURE 4e.—Discontinuous uniform crystal growth forming rings in the broken otolith. Scale bar = 0.1 mm.
f.—Fine and deep (arrowed) increments on the polished and etched otolith surface. Scale bar = 0.1 mm.

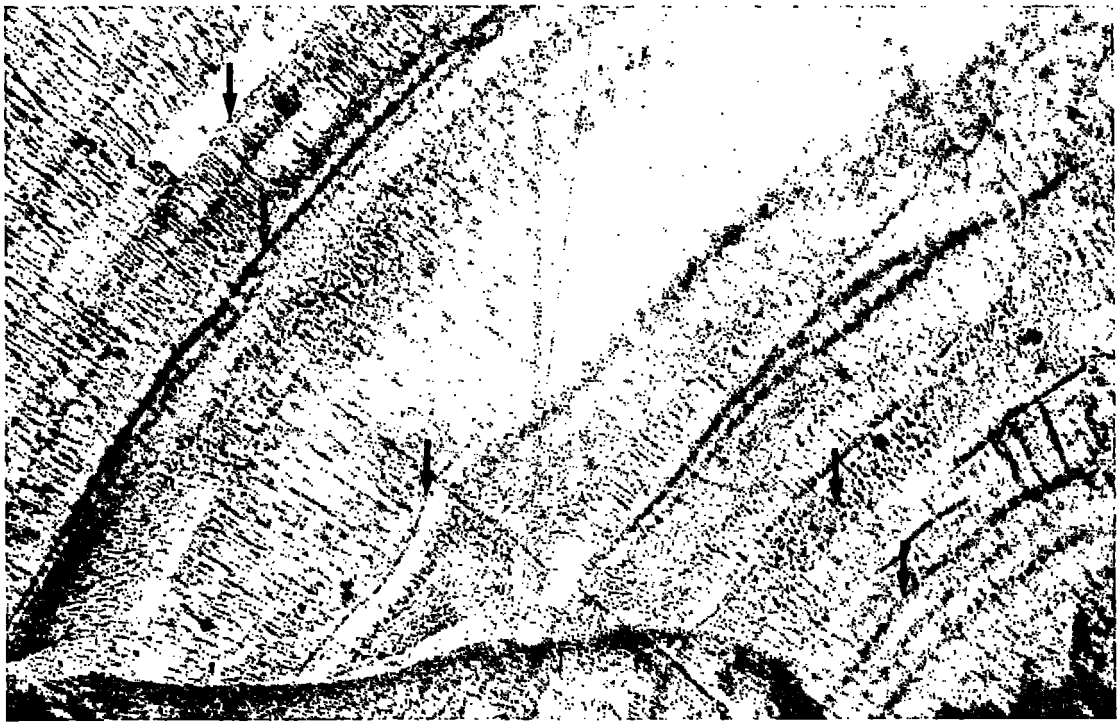
g



h

FIGURE 4g.—Fine increments obscured by coarse crystallinity on the polished and etched otolith surface. Scale bar = 10 µm.
h.—Fine increments (arrowed) found between widely spaced large rings in the otolith cross-section. Magnification = 72×.

i



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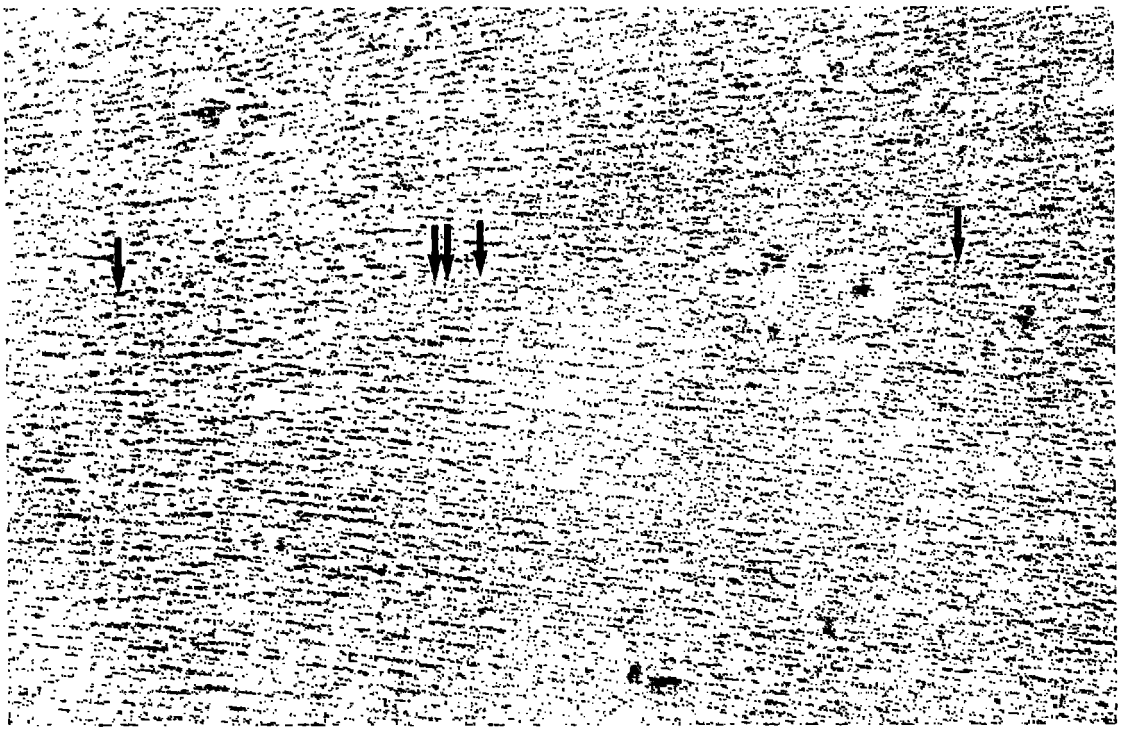

FIGURE 4i.—Variation of increment widths (arrowed) in the otolith cross-section. Magnification = 160×.

j.—Cellulose-acetate peel showing the intermittency of fine increment sequences (arrowed), often obscured by a coarse underlying crystallinity. Magnification = 160×.

becomes difficult to determine because of the intermittent nature of the growth increments and the variety of width-sizes (Fig. 4i). In large areas of the otolith, increments appear to be absent or indeterminate, with a coarse underlying crystal structure (Fig. 4j) making accurate determination of increment sequences difficult. However, the fine increments of the oreo otolith are 3 to 5 μm wide, which is within the range of daily growth increments described for other species (Jones 1986; Gauldie in press).

Black Oreo Otolith

The black oreo otolith is almost identical to that found in the smooth oreo in overall shape, proportion, structure, topography, surface and internal crystallinity, and increment pattern. Some minor differences do, however, exist.

In the medial sulcus, the prominent knobs found in the smooth oreo otolith are smaller than in the black oreo. On the surface of the sulcus, large leaflike crystals having various orientations occur (Fig. 5a). Also present in the sulcus are porous, sponge-like crystals adjacent to membranous structures (Fig. 5b). Smooth patches, where crystals appear absent, occur on the lateral surface of the otherwise coarsely crystalline irregular lobe (Fig. 5c). At higher magnification the smooth patches are seen to be smaller growth forms of the larger adjacent crystals.

DISCUSSION

Despite some minor differences in topography and crystallinity, the sagittae of both species are essentially identical. The otoliths are structurally complex with a great variety of crystalline forms. The coarse

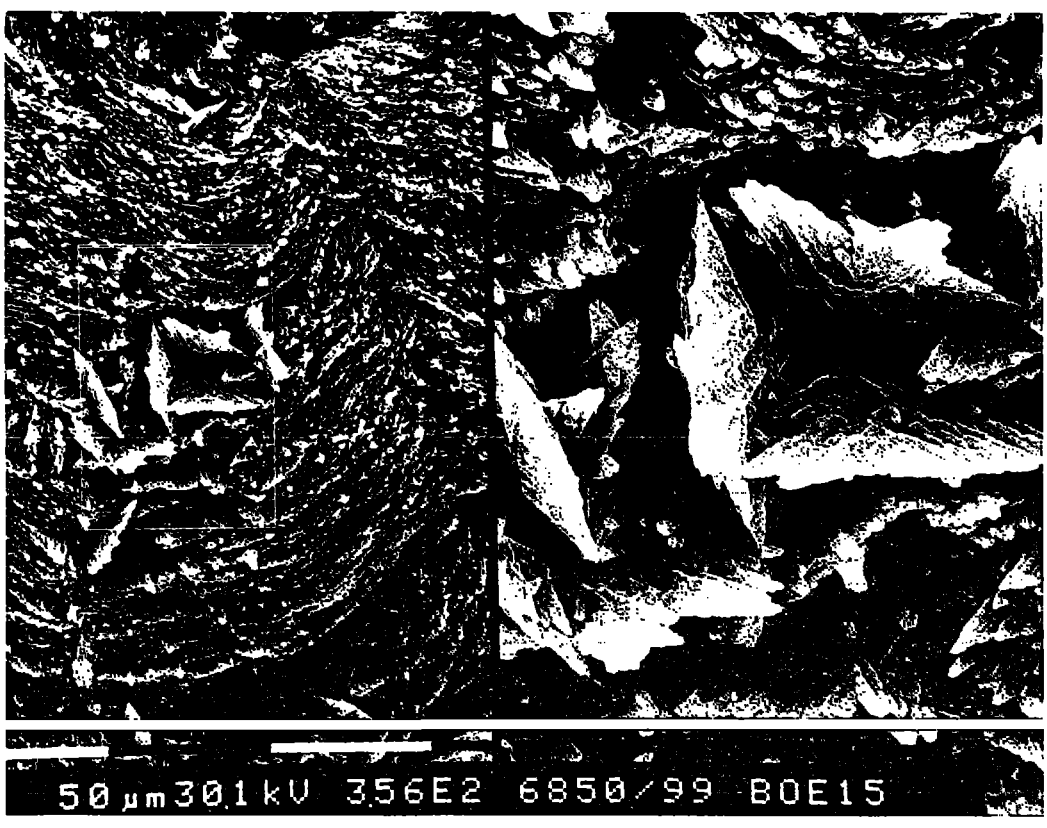

FIGURE 5a.—Split-screen SEM of large leaflike crystals in the black oreo otolith sulcus. Magnification = 356× and 979×.

b.—Porous, sponge-like crystals in the otolith sulcus. Scale bar = 10 μm.

c.—Smooth patches on the central lateral surface of the otolith. Scale bar = 0.1 mm.

b

10µm30.0kV 2.20E3 7170/99 BOE20A

c

0.1mm30.0kV 1.70E2 7172/99 BOE20A

crystals on the central lateral surface are comparable with those in the oyster shell described as individual laths (Carriker et al. 1980). The leaflike crystals in the sulcus of the black oreo otolith are similar to the chalky crystal forms in the oyster shell (Carriker et al. 1980). Such a variety of crystalline forms is uncommon in teleost otoliths. The low legibility of structures of various kinds in the otolith may reflect this complex crystallinity. However, the complex crystallinity of the mollusc shell is thought to reflect changes in both the external and internal milieu of the organism (Wilbur and Saleuddin 1983). Thus the difficulties of reading the oreo otolith in the conventional sense may be offset by the life history record (albeit difficult to translate) provided by its complex crystallinity.

The broken sections of the otolith reveal the internal structure organization, and development of crystals. Epitaxial crystal growth in the oreo otolith results in columnar, monoclinal crystals of aragonite. However, the presence of calcite-like prisms has not been described for other otoliths. Calcite occurs on the antisulcal surface of some otoliths apparently by simple crystallization out of the fluid of the endolymphatic sac (Morales-Nin 1985), but calcite has never been described from within an aragonite otolith (Carlstrom 1963). In molluscs, calcite replacement of aragonite results in an orderly alignment of calcite crystals following the alignment of the original aragonite crystals. The disorderly appearance of the calcite-like hexagons in the smooth oreo otolith may be due to a diagenetic transformation of aragonite to calcite with depth. The compensation depth for the aragonite/calcite transformation is about 3,000 m (Fyfe and Bischoff 1965) well beyond the known range of the smooth oreo which has a maximum recorded depth of 1,300 m. However, there may be enough variation in either the kind or amount of stabilizing protein in the smooth oreo otolith to allow crystal changes to occur at shallower depths than 3,000 m.

The complex, and often coarse, crystal structure of the oreo otolith obscures the sequences of increments when they do occur. As a result, large rings observed at low magnification become indistinct at higher magnification when many finer increments appear. The large rings could be assumed to be annual check rings, but the difficulties in differentiating between the fine and large rings create ambivalence in one's interpretation. The finer microscopic growth increments, analagous to daily growth rings, have no uniform width and occur intermittently making accurate counting impossible.

The suitability of an otolith for determining the age of a fish depends on the pattern of both annual and daily check rings inferred from the structure of the otolith. The hyaline/opaque zones observed in the regular lobe (using transmitted light) had a similar mean width to the concentric ridges found by SEM on the lateral surface. The *t*-statistic we obtained accepts the null hypothesis that no significant difference exists between the two means. Mel'nikov (1981) regarded these opaque/hyaline zones as annual check rings in the otolith of *Allocyttus verrucosus*. However, because no evidence exists for a relationship between the surface ridges and fish age, it is possible that Mel'nikov's (1981) ages are incorrect. Furthermore, the width of the opaque/hyaline zones (0.34 mm) would indicate daily growth increments less than 1 μm wide. There are no reports in the literature of validated daily growth rings of such small size. In addition, the microscopic growth increments which we have observed in the oreo otolith are 3 to 5 μm wide, which is a size range commonly observed in other species.

With the techniques available we have been unable to use either annual- or daily-type structures to develop a technique for age estimation for *Pseudocyttus maculatus* and *Allocyttus* sp. The reasons for these difficulties may lie in the crystal morphology of the otoliths which are more complex than any so far described in the literature.

ACKNOWLEDGMENTS

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RELATIONSHIP BETWEEN SEDIMENT CHARACTER AND SEX SEGREGATION IN ENGLISH SOLE, *PAROPHRYS VETULUS*[1]

D. SCOTT BECKER[2]

ABSTRACT

English sole, *Parophrys vetulus*, were collected by otter trawl in the nearshore zone of Puget Sound, Washington, during two surveys conducted in 1981–82 and 1984. Stations in both surveys were distributed across a broad range of sedimentary environments. Sex segregation by English sole was strongly associated with the grain-size characteristics of bottom sediments. This association was persistent across a variety of sampling conditions, including different years, seasons, embayments, and depths. Fish age did not appear to influence the observed association. Results of this study provide the first documentation of the influence of sediment character on sex segregation by a pleuronectid, and suggest that this relationship should be considered in future studies of English sole and, perhaps, other pleuronectids as well.

Sex segregation by fishes of the family Pleuronectidae (i.e., righteye flounders) has been documented for numerous species from the United States (Alverson and Chatwin 1957; Fadeev 1970; Alton 1972), Europe (Rae 1965), and Asia (Moiseev 1953; Kovtsova 1982). These patterns have been related to such factors as geographic location, depth, season, and age of fish. However, because most of these observations have been made while fishes were being collected for other purposes, the underlying reasons for the observed patterns are poorly understood.

Several studies have documented sex segregation in English sole, *Parophrys vetulus*, a pleuronectid found in nearshore areas along the west coasts of the United States and Canada (Hart 1973). In describing the catch of the English sole fishery in Hecate Strait, British Columbia, Ketchen (1956) noted that considerable sex segregation takes place, particularly during the summer months. In a study of the population characteristics of this species in Puget Sound, Holland (1969) found a difference of 18% between the percentages of males in the populations from two locations. Because both of these accounts were largely anecdotal, no evaluations of the observed patterns were made.

One factor that has yet to be evaluated with respect to sex segregation by pleuronectids is the character of bottom sediments. Because pleuronectids live in close association with the sea floor, it might be surmised that the characteristics of that environment exert a differential influence on the distributions of the two sexes. Additional support for this hypothesis comes from the fact that the influence of sediment character on the overall distribution (i.e., both sexes pooled) of several pleuronectids has been well documented (Ketchen 1956; Alverson et al. 1964; Feder et al. 1974; Pearcy 1978; Scott 1982; Becker 1984).

In this paper, I evaluate patterns of sex segregation by English sole in relation to the character of bottom sediments in nearshore areas of Puget Sound, WA. This study provides the first determination of how sediment character influences sex segregation in a pleuronectid. In relating sediment character to sex segregation in English sole, I also evaluate the potential influences of depth, season, and fish age on the observed relationships.

METHODS

English sole were sampled during two independent surveys conducted in several embayments of Puget Sound in 1981–82 and 1984. The relationship between sex segregation and sediment character was evaluated separately for each survey. Although the two surveys differed with respect to such variables as station locations, sampling times, and sample sizes, the basic collection and analytical methods used in both surveys were similar.

In both surveys, the sex ratio of the English sole captured at each station was represented by the proportion of the sample comprised of males (i.e., male proportion). Sediment character at each station was represented by the percentage (by weight) of the

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grain-size distribution comprised of fine-grained material (i.e., <0.063 mm in size). This variable was used as an index of sediment character because many physical, chemical, and biological characteristics of sedimentary environments covary with the grain-size distribution (Buchanan 1984).

During 1981–82, English sole were collected from 15 May to 6 July 1981 at 12 transects in Commencement Bay, Elliott Bay, and Sinclair Inlet (Fig. 1). Fishes also were collected during three additional time periods (23–24 November 1981; 8–9 March 1982; 30–31 August 1982) to evaluate seasonal patterns at three stations in Commencement Bay (CB-1, CB-4, and CB-5; Fig. 1). These stations were selected to represent a gradient of sediment grain size. Although the seasonal sampling occurred over a 2-yr period, it was assumed that interannual variation was not sufficiently large to obscure major seasonal patterns.

During the May–July sampling, English sole were collected at each transect during morning (07:00–09:30), midday (10:00–13:30), evening (20:30–23:30), and midnight (00:30–04:00). During the remaining sampling periods, fish were collected only during midday and evening. For each transect, results obtained for different periods of the diel cycle were pooled before male proportions were calculated. Sex determinations and evaluations of spawning condition were made for all English sole larger than 160 mm total length (TL). Age was not determined.

During 1984, English sole were collected from 4 to 9 June 1984 at 15 transects in Commencement Bay and at 2 transects in Carr Inlet (Fig. 1). Sampling was conducted during daylight hours (06:30–17:00) at all transects. Sex determinations and evaluations of spawning condition were made for all individuals larger than 225 mm TL. Age was determined by otolith analysis for all fish.

During both surveys, English sole were collected using a 7.6 m (headrope) Marinovich otter trawl having a body mesh of 3.2 cm (stretched) and a cod end liner mesh size of 0.8 cm (stretched). Trawling was conducted along isobaths at a constant vessel speed of approximately 2.5 knots.

During both surveys, bottom sediments were sampled using a modified van Veen bottom grab and the grain-size distribution of the top 2 cm of sediment was determined using standard sieve and pipette techniques (Folk 1968). During 1981–82, sediments were collected at five sampling points located at approximately equal distances along each transect. During 1984, sediments were collected at a variable number of stations located within 300 m from each transect.

The association between percent fine-grained sediment and male proportion of English sole was tested using Spearman's rank correlation coefficient (r_s). The association between station depth and male proportion was tested in the same manner. Differences in male proportion among age-classes of fish and among the seasonal sampling transects were tested using the G-test (Sokal and Rohlf 1981).

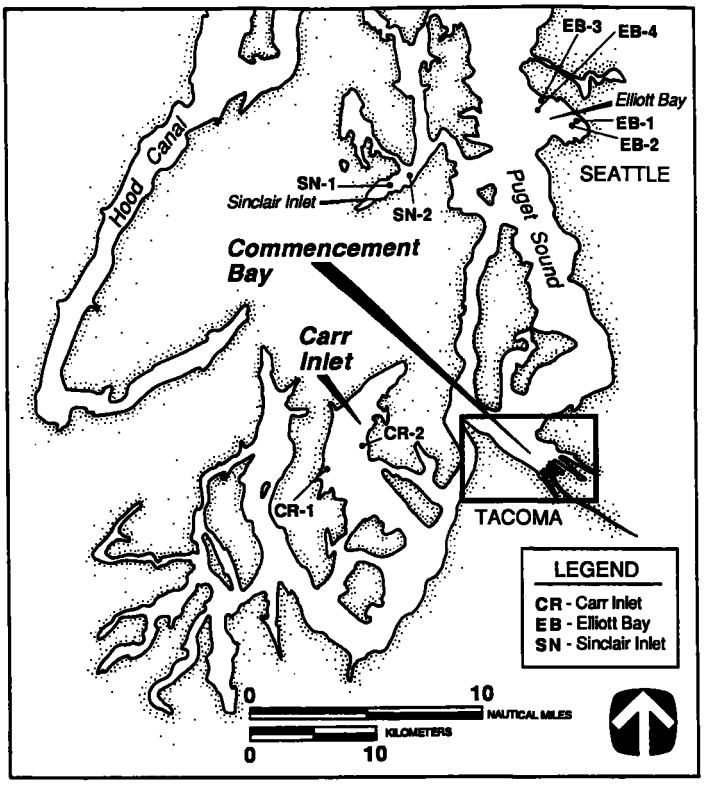
RESULTS

Station depth, percent fine-grained sediment, sample size, and male proportion at each transect from the 1981–82 and 1984 surveys are presented in Tables 1 and 2, respectively. During 1981–82, 4,430 English sole were sampled from stations ranging in depth from 8 to 36 m. Percent fine-grained sediment ranged from 5.8 to 92.1% and male proportion ranged from 0.20 to 0.91. During 1984, 1,007 English sole were collected from stations ranging in depth from 5 to 20 m. Percent fine-grained sediment ranged from 8.6 to 87.5% and male proportion ranged from 0.13 to 0.98.

The correlation between percent fine-grained sediment and male proportion of English sole was significant ($P \leq 0.01$; $r_s = 0.73$) for the May–July sampling of the 1981–82 survey (Fig. 2). This correlation was also significant ($P \leq 0.001$; $r_s = 0.80$) for the 1984 survey (Fig. 2). Correlations between depth and male proportion were not significant ($P > 0.05$) for either the 1981–82 ($r_s = -0.10$) or 1984 ($r_s = -0.04$) survey.

For the stations sampled seasonally in 1981–82 (CB-1, CB-4, and CB-5), heterogeneity of male proportion among stations was significant ($P \leq 0.05$) during all four sampling periods (Fig. 3). In all cases, male proportion was lowest at CB-5, highest at CB-4, and intermediate in magnitude at CB-1. This gradient of increasing male proportion was consistent with the gradient of increasing percent fine-grained sediment at the three stations (Table 1). The mean abundance of English sole at the three stations rose from a minimum level in March to a peak in May–July, and then declined through August to a level in November that was similar to that in March (Fig. 3).

For both surveys combined, 64 (1.2%) English sole were found to be in spawning condition. Twenty-four of those individuals were collected during March, to represent a spawning component of 14.8% during that month. The remaining 42 individuals were sampled between May and July to represent



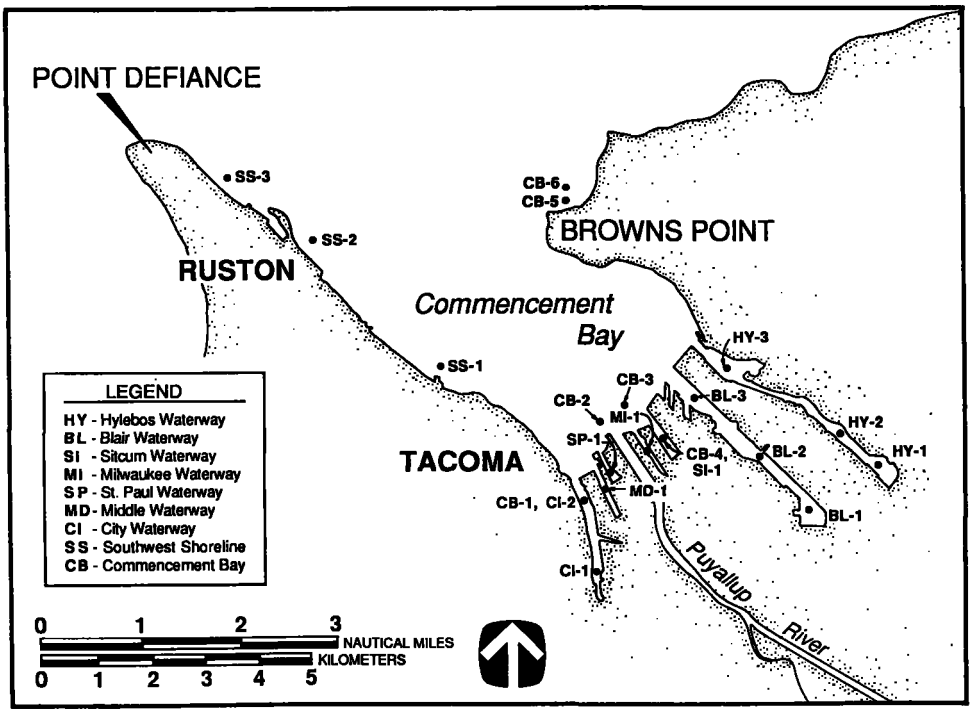


FIGURE 1.—Locations of transects sampled in 1981–82 (denoted by CB, EB, and SN) and 1984 (all remaining transects).

TABLE 1.—Characteristics of transects and samples of English sole during 1981–82.[1]

Station[2]	Depth (m)	Mean percent fine-grained sediment[3]	Sample size[4]				Male proportion			
			May–July	August	November	March	May–July	August	November	March
CB-1	10	27.1	655	249	65	90	0.83	0.74	0.58	0.57
CB-2	33	47.0	554				0.78			
CB-3	36	44.2	160				0.79			
CB-4	14	71.6	589	146	174	38	0.91	0.82	0.77	0.87
CB-5	13	7.6	181	67	68	35	0.55	0.64	0.44	0.20
CB-6	35	11.2	128				0.66			
EB-1	14	56.0	82				0.68			
EB-2	31	76.2	17				0.76			
EB-3	16	5.8	90				0.53			
EB-4	32	8.8	49				0.49			
SN-1	8	92.1	683				0.84			
SN-2	10	13.7	310				0.30			

[1]Sampling in May–July and November was conducted in 1981, whereas sampling in August and March was conducted in 1982.
[2]Locations of transects are presented in Figure 1.
[3]Each value is based on five replicate samples.
[4]All English sole were larger than 160 mm TL.

TABLE 2.—Characteristics of transects and samples of English sole during 1984.

Station[1]	Depth (m)	Mean percent fine-grained sediment[2]	Sample size[3]	Male proportion
CR-1	18	14.5 (2)	60	0.28
CR-2	12	8.6 (2)	60	0.13
SS-1	9	18.2 (2)	59	0.29
SS-2	10	22.9 (6)	60	0.48
SS-3	20	8.7 (6)	60	0.35
CI-1	5	68.8 (4)	57	0.75
CI-2	9	58.2 (4)	52	0.73
MD-1	6	40.4 (2)	59	0.42
SP-1	5	48.9 (3)	60	0.77
MI-1	10	87.5 (5)	60	0.87
SI-1	12	73.8 (5)	60	0.98
BL-1	11	55.2 (1)	60	0.77
BL-2	12	74.3 (9)	60	0.88
BL-3	10	55.4 (6)	60	0.88
HY-1	9	68.1 (5)	60	0.45
HY-2	9	79.8 (7)	60	0.80
HY-3	9	61.1 (12)	60	0.73

[1]Locations of transects are presented in Figure 1.
[2]Number of stations used to calculate mean percent fine-grained sediment at each transect is given in parentheses.
[3]All English sole were larger than 225 mm TL.

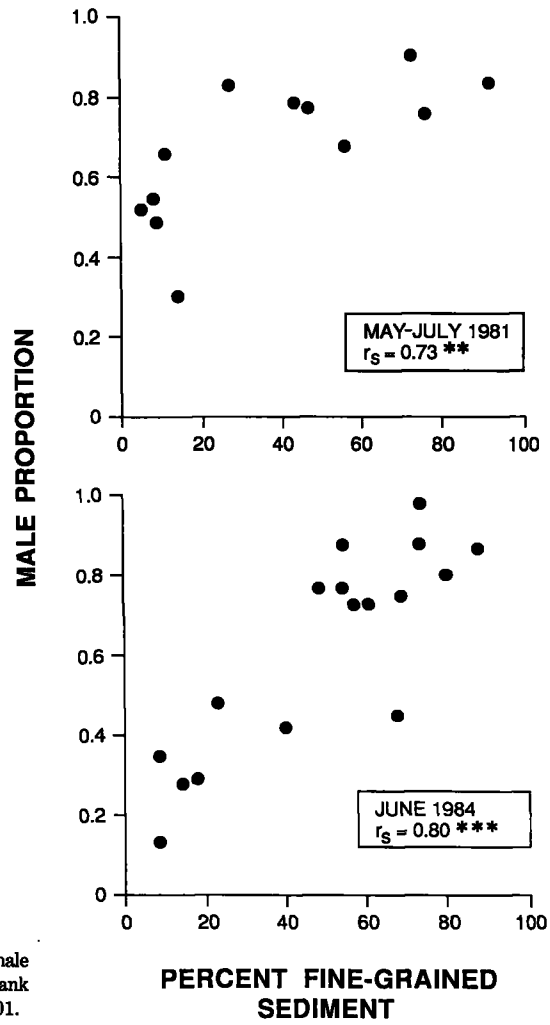


FIGURE 2.—Comparison of percent fine-grained sediment and male proportion of English sole populations using Spearman's rank correlation coefficient (r_s). ** = $P \leq 0.01$, *** = $P \leq 0.001$.

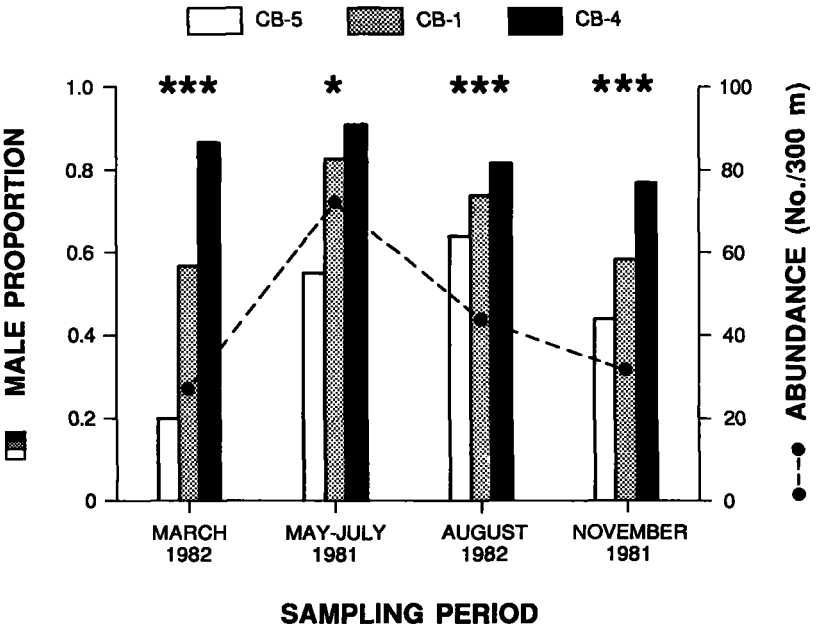


FIGURE 3.—Comparisons of male proportion of English sole populations at three Commencement Bay stations during four sampling periods using the *G*-test. Mean abundance of English sole at all three stations is plotted for each sampling period. The values of percent fine-grained sediment at Stations CB-5, CB-1, and CB-4 were 7.6%, 27.1%, and 71.6%, respectively. * = $P \leq 0.05$, *** = $P \leq 0.001$.

a spawning component of 0.9% during that period. No fish were found to be in spawning condition during August and November.

For English sole aged 3–10 years old during the 1984 study, male proportion for each age-class ranged from 0.50 to 0.66 (Fig. 4). However, the heterogeneity among age-classes was not significant ($P > 0.05$). Nineteen fish aged 2 or >10 years old were not included in this analysis because sample sizes by age-class were too small.

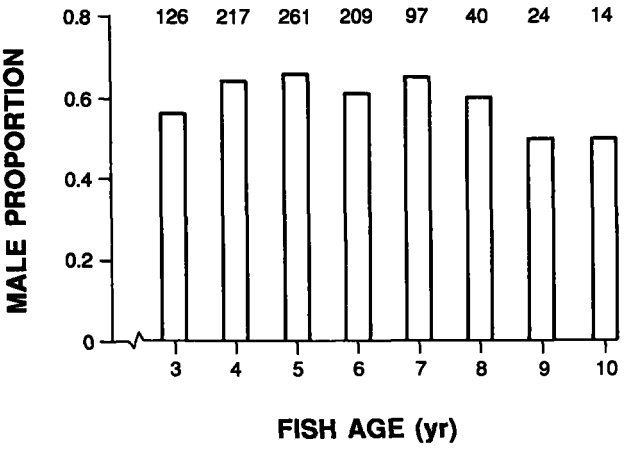


FIGURE 4.—Comparison of male proportion among age-classes of English sole collected in 1984. Sample size is presented above each bar.

DISCUSSION

Results of this study demonstrate that sex segregation by English sole in nearshore areas of Puget Sound is strongly associated with the grain-size distribution of bottom sediments. In addition to the results of statistical analyses, the strength of this association is demonstrated by its persistence across a variety of sampling conditions. For example, the association was found in two independent surveys conducted 2–3 years apart. Furthermore, the 1981–82 survey represented an analysis of large-scale patterns across three embayments, whereas the 1984 survey focused on small-scale patterns within a single embayment. The association between sex segregation and sediment grain size also persisted across seasons and across a range of depth.

Although a significant association was found between sediment grain size and male proportion of English sole, a variety of factors that covary with sediment grain size may have been partly or totally responsible for this association (Lagler et al. 1977; Moyle and Cech 1982). Examples of physical/chemical variables that often covary with grain size and may influence fish distributions include depth, current speed, turbidity, and dissolved oxygen. Examples of biological factors include the composition of prey assemblages and the distribution of predators. Although results of this study demonstrated that depth did not influence the observed association between sediment grain size and male proportion, further experimentation is required to identify the factor or suite of factors that directly influences sex segregation in this species.

Despite the fact that depth did not influence the patterns of sex segregation identified for English sole, the range of depth considered in this study (5–36 m) is a small fraction of the total range occupied by this species (0–550 m; Hart 1973). It therefore is possible that depth-related sex segregation in this species may be observed if a wider range of depths were examined. For example, considerable sex segregation by depth was found for Dover sole, *Microstomus pacificus*, off the west coast of the United States when a large depth range (110–440 m) was evaluated (Hagerman 1952; Alton 1972).

Based on results of the 1984 survey, no relationship between age and male proportion in English sole was evident. It therefore is unlikely that age influenced the observed relationship between male proportion and sediment grain size. A decline in male proportion with increasing age has been found for several pleuronectids (Rae 1965; Kovtsova 1982). Because most of the fish examined in this study were relatively young (<8 years old) compared with the maximum age of 15–17 years sometimes reached by individuals of this species (Ketchen 1956; Holland 1969; Van Cleve and El Sayed 1969), consideration of older fish may alter the patterns observed in this study. Although sample sizes for fish aged 9–10 years were relatively small in this study, male proportion in those age groups (0.50) was lower than that observed in all younger age groups (0.57–0.66).

The season of sampling did not alter the observed relationship between male proportion and sediment grain size. This relationship remained intact despite the fact that the mean abundance of English sole changed substantially throughout the seasonal cycle. The observed seasonal changes in mean abundance are consistent with the seasonal pattern of migration exhibited by adults of this species and most other pleuronectids. That pattern includes a migration to deeper water in the fall for overwintering and spawning, and a return migration to shallower water in spring for feeding throughout the summer (Ketchen 1956; Alverson et al. 1964; Roff 1982). It is unlikely that spawning substantially influenced the observed seasonal patterns of sex segregation in English sole, because the largest percentage of fish in spawning condition during any season was <15%. However, sex segregation in relation to spawning in pleuronectids has been documented for several species (Moiseev 1953; Alverson and Chatwin 1957), and may influence sex segregation in English sole when a substantial percentage of the population is in spawning condition.

Results of this study suggest that the influence of sex segregation should be considered when characteristics of English sole populations are compared among habitats that differ with respect to sediment character. Patterns based on population characteristics capable of exhibiting a dependence on sex (growth, condition, disease prevalence, tissue contamination) could be strongly biased if differences in the sex ratio among stations are not considered. This concern should probably be extended to studies of other pleuronectids, because the relationship between sex segregation and sediment character is unknown for most species.

Although the reasons for the observed patterns of sex segregation in English sole are unknown, a potential explanation is that different energetic needs induce male and female fish to utilize different habitats. Female English sole grow to a larger size than males and mature at an older age (Ketchen 1956; Holland 1969; Van Cleve and El-Sayed 1969; Hart 1973). In addition, fecundity in females is proportionate to individual size (Ketchen 1956; Hart

1973). These patterns are found for numerous pleuronectids and are thought to allow females to outgrow predators and maximize fecundity (Roff 1982). Female English sole may therefore select different habitats than males to support their differential reproductive requirements. Because many characteristics of benthic macroinvertebrate assemblages (i.e., the primary prey of English sole) are related to sediment character (Gray 1974; Rhoads 1974; Pearson and Rosenberg 1978), selection of habitats that differ in sediment grain size provides females with different prey spectra and energetic potentials than are available to males. In addition, differential habitat selection would reduce the potential of competition for food between sexes.

In summary, sex segregation by English sole was strongly associated with the grain-size characteristics of bottom sediments. This association was persistent across a variety of sampling conditions, including different years, seasons, embayments, and depths. Fish age did not appear to influence the observed association. Results of this study provide the first documentation of the influence of sediment character on sex segregation in a pleuronectid, and suggest that this relationship should be considered in future studies of English sole and, perhaps, other pleuronectids as well.

ACKNOWLEDGMENTS

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OCCURRENCE OF *CANCER* CRAB (*C. MAGISTER* AND *C. OREGONENSIS*) MEGALOPAE OFF THE WEST COAST OF VANCOUVER ISLAND, BRITISH COLUMBIA

GLEN S. JAMIESON AND ANTAN C. PHILLIPS[1]

ABSTRACT

The seasonal and cross-shelf occurrences of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae in 1985 along a transect line perpendicular to the coast off Tofino, British Columbia, are presented. Megalopae of both species were generally absent from surface waters during daylight hours. The two species may have slight temporal differences in nocturnal surface abundance, with *C. magister* occurring later in the evening and earlier in the morning than *C. oregonensis*. Their relative occurrence at the surface during the night was used to calibrate cross-shelf megalopal abundance data. Cross-shelf megalopal intermolt stage proportions were calculated, relating degree of megalopal development to proximity of nearshore habitat required for successful settlement of larvae.

Cancer magister megalopae were present from April to August, with peak abundance in May and June. Megalopae were abundant in a broad band 37–148 km from shore, with peak abundance (2,871 10 m^{-2}) 56 km offshore in June. In May, some late stage megalopae were collected in coastal inlets but settlement appeared low in coastal study areas. Megalopal abundance decreased abruptly shoreward of 28 km from the coast.

Cancer oregonensis megalopae were also present from April to August, with their pattern of cross-shelf abundance basically similar to that of *C. magister*. However, in contrast to *C. magister*, abundance of late stage megalopae in coastal inlets was relatively high (313 10 m^{-2}) in June, indicating that a significant settlement of megalopae of this species could have occurred.

Evidence for cross-shelf movement of *Cancer* megalopae is discussed.

Dungeness crab, *Cancer magister*, range from the Aleutian Islands to northern Mexico in the eastern Pacific (Hart 1982) and are commercially exploited from northern California to Kodiak Island, AK. As part of an ongoing study of Dungeness crab recruitment off the west coast of Vancouver Island, the abundance and distribution of larvae off Tofino, British Columbia, are being studied to determine how variability in annual recruitment is affected by larval settlement.

Dungeness crab larvae are planktonic and pass through five zoeal stages and one megalopal stage before settling to the sea bottom. Studies of larvae prior to the 1970s primarily involved descriptions of larval morphology (Mir 1961; Poole 1966), and it was not until Reed (1969) developed laboratory culture methods that larval environmental requirements were first described. Optimal ranges of temperature and salinity for laboratory-cultured zoeae were 10.0°–13.9°C and 25–30‰ respectively, but their survival was not significantly affected by the temperature and salinity ranges occurring in the waters off Oregon, where Reed's study was conducted, at the time of year when larvae are commonly found. Lough (1976) suggested offshore larval movement would allow larvae to avoid lower nearshore salinities, and that normal oceanic salinity levels probably favor survival over the long term.

The temporal occurrence of larvae in open coast oceanic waters varies somewhat according to latitude, with larvae present earliest in the season in the southern part of the species' range. Seasonal occurrence has not been well documented in the inshore waters of Georgia Strait, Puget Sound, and Juan de Fuca Strait, but appears to differ significantly from that in open coast waters. Larval settlement, which typically occurs in May and June off the outer coast of Washington, can occur as late as mid-September in northern Puget Sound (D. Armstrong[2]).

Temporal and spatial distributions of crab larvae have been documented for the years 1975–80 in the Gulf of Farallones and the San Francisco-San Pablo-Suisun Bay complex in central California (Reilly

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1983) and for the years 1969–70 along a transect off Newport, OR (Lough 1975, 1976). These studies suggest that while larvae are hatched in the nearshore, shallow-water environment preferred by adult Dungeness crab, they subsequently move alongshore and offshore, and then inshore, often over considerable distances. Larvae hatched off California and Oregon in late winter have been hypothesized to move northward with the Davidson Current before its reversal in March-April, and offshore as a result of upwelling, Ekman transport, estuarine runoff, and geostrophic flow, depending on location and season (Lough 1976; Wild and Tasto 1983). Later stage zoeae are typically found progressively further offshore, and it seems to be the megalopal stage that returns inshore (Lough 1976; Reilly 1983). The megalopal stage is the strongest swimming stage (Jacoby 1982), but there is no direct evidence to indicate that their inshore movement is active.

There are five species of crabs of the genus *Cancer* in British Columbia (Hart 1982), and larvae of *C. oregonensis* also occur in abundance in offshore waters along with *C. magister* (Lough 1975). *Cancer oregonensis* has no commercial importance, but since it occurs with *C. magister*, data on both species of crabs are included in this study. Comparisons of occurrence between the two species may provide insight into possible environmental mechanisms or processes that influence transport from offshore areas to the inshore juvenile habitats, which the larvae of both species must reach.

This study establishes the seasonal and spatial occurrences of *Cancer* megalopae along a transect over and beyond the continental shelf off the west coast of Vancouver Island (Fig. 1). The geographical area is of particular interest because of the location of a major regional crab fishery near Tofino (Jamieson 1985; Noakes and Jamieson 1986) and the resulting importance of understanding factors influencing the magnitude of local larval crab settlement. The oceanography off Vancouver Island has been relatively well studied (Freeland et al. 1984; Thomson 1981), and because of the intrusion of Juan de Fuca Strait waters into the general longshore oceanographic regime and the relative increase in topographical complexity of the continental shelf, it is considerably more complicated than that found

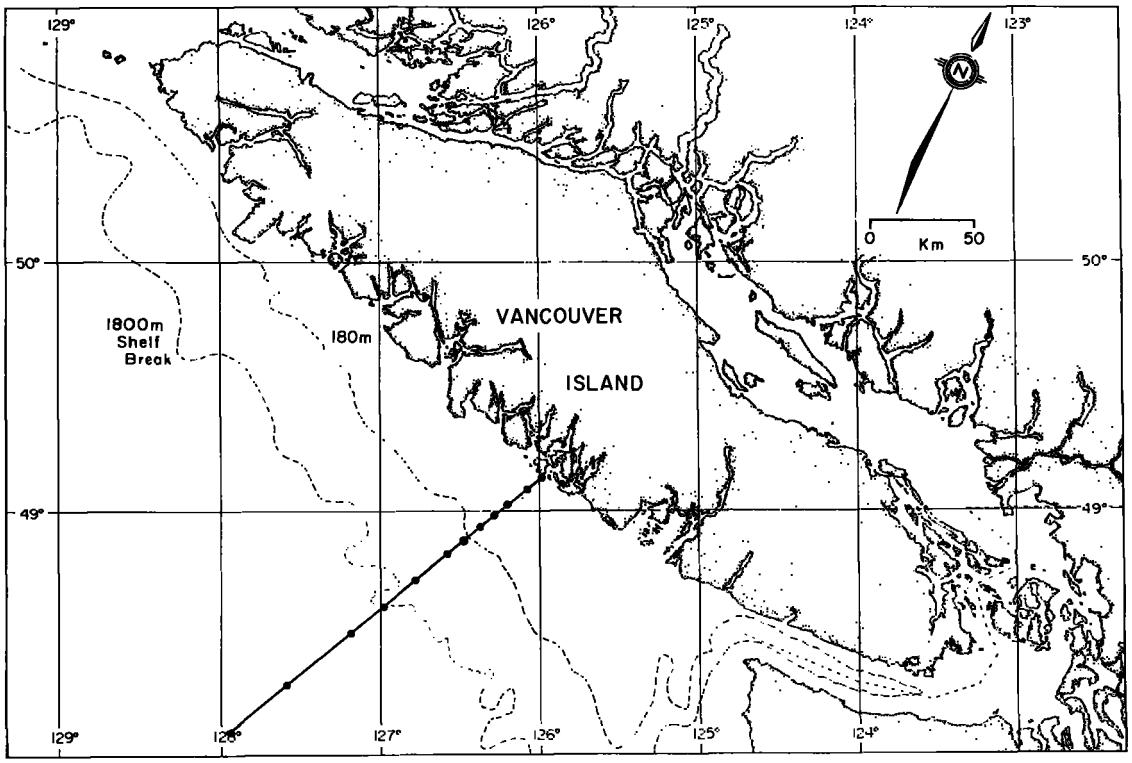

FIGURE 1.—The survey transect line, with stations, over which this study was conducted.

south of Cape Flattery (Hickey 1979). Along the eastern Pacific coast, Cape Flattery marks a significant change in nearshore oceanography, and this study to investigate larval crab distribution in open coast waters is the first one north of this landmark.

GENERAL OCEANOGRAPHY OFF VANCOUVER ISLAND

A seasonal surface current moving northward from about lat. 32°N to 51°N (northern Vancouver Island) typically exists in nearshore waters from October to March (Fig. 2). South of Cape Flattery, this is called the Davidson Current (Hickey 1979) whereas off British Columbia, it appears to consist of two components. Nearshore, there is the year-round, northward flowing Vancouver Island Coastal Current, about 20–30 km wide, and further offshore, there is the seasonal Shelf-Break Current, perhaps a continuation of the Davidson Current, which reverses direction in response to changes in the large-scale wind field (Freeland et al. 1984). The Davidson Current off Oregon has an average northward flow of 50 cm/s for 30% of the time (Boisvert 1969), sufficient to transport larvae significant distances northward during their developmental period if they remained continuously in the current. The California Current is a seasonal, southward moving, surface current of similar magnitude and location to the Davidson Current. It occurs off Vancouver Island (Hickey 1979) in the spring and summer, along with the seasonal, southward flowing, Shelf-Break Current on the outer continental shelf (Freeland et al. 1984). These currents could transport larvae located off Vancouver Island during the spring and summer southwards (Fig. 2). North of Vancouver Island, outer continental shelf currents are poorly described, but off Cape St. James (southern tip of the Queen Charlotte Islands), the surface flow is strongly southward almost year-round, turning northward only in March and April (Freeland et al. 1984). The Vancouver Island Coastal Current originates at the mouth of Juan de Fuca Strait, and so could transport larvae out of the Puget Sound-Georgia Strait complex.

MATERIALS AND METHODS

General Methodology

Sampling was largely done along an offshore transect line perpendicular to the coast off Tofino, British Columbia (Fig. 1), with stations located at 0, 9.3, 18.5, 27.8, 37, 46, 55.6, 74.1, 92.3, 111.2, 148.2, and 185.3 km from shore. Stations were more closely spaced nearshore where larval abundance was expected to be greatest, but the transect extended well beyond the shelf break to determine what the seaward distribution of megalopae might be.

Six offshore samplings were made along the transect from February through August 1985, but only three extended the full 185 km. Dates of sampling were 27 February–4 March, 17 and 18 April, 30 and 31 May, 14 and 15 June, 6 and 7 July, and 24 and 25 August. February–March, June, and July samplings were terminated 74 km, 130 km, and 111 km offshore, respectively, because of poor weather and time constraints.

At each station, a neuston tow and an oblique bongo tow to 250 m, or to within 5 m of bottom, were made, and a temperature profile was recorded by means of an expendable bathythermograph. On all cruises, bongo tows were done during daylight hours and neuston tows at night; late-stage crab larvae congregate near the water surface at night (Booth et al. 1985). On 17 June 1985, an hourly, nocturnal series of neuston tows was made at one location, 9.3 km offshore, to identify patterns of nighttime abundance of megalopae in surface waters.

To supplement offshore sampling along the transect, neuston tows were made after dusk in the inlets around Tofino biweekly from early May through August 1985 to monitor presence and movement of larvae. In addition, a beam trawl and epibenthic sled were used in inshore waters in July 1985 to sample for newly settled larvae in an effort to establish time and magnitude of larval settlement.

The RV *G. B. Reed* was used for all offshore sampling except for the June sample, which was collected from a 27 m charter vessel. Inshore sampling was conducted from a 7 m aluminum herring skiff except for mid-June, when the charter vessel was again used.

Gear

The neuston sampler was a modified otter surface sampler (Mason and Phillips 1986) with a square mouth opening 45 cm on each side; under calm sea conditions, it sampled the top 35 cm of the water column. A General Oceanics flowmeter[3] in the mouth of the net was used to establish volume of water filtered. Netting was black, 500 μ Nitex, and

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

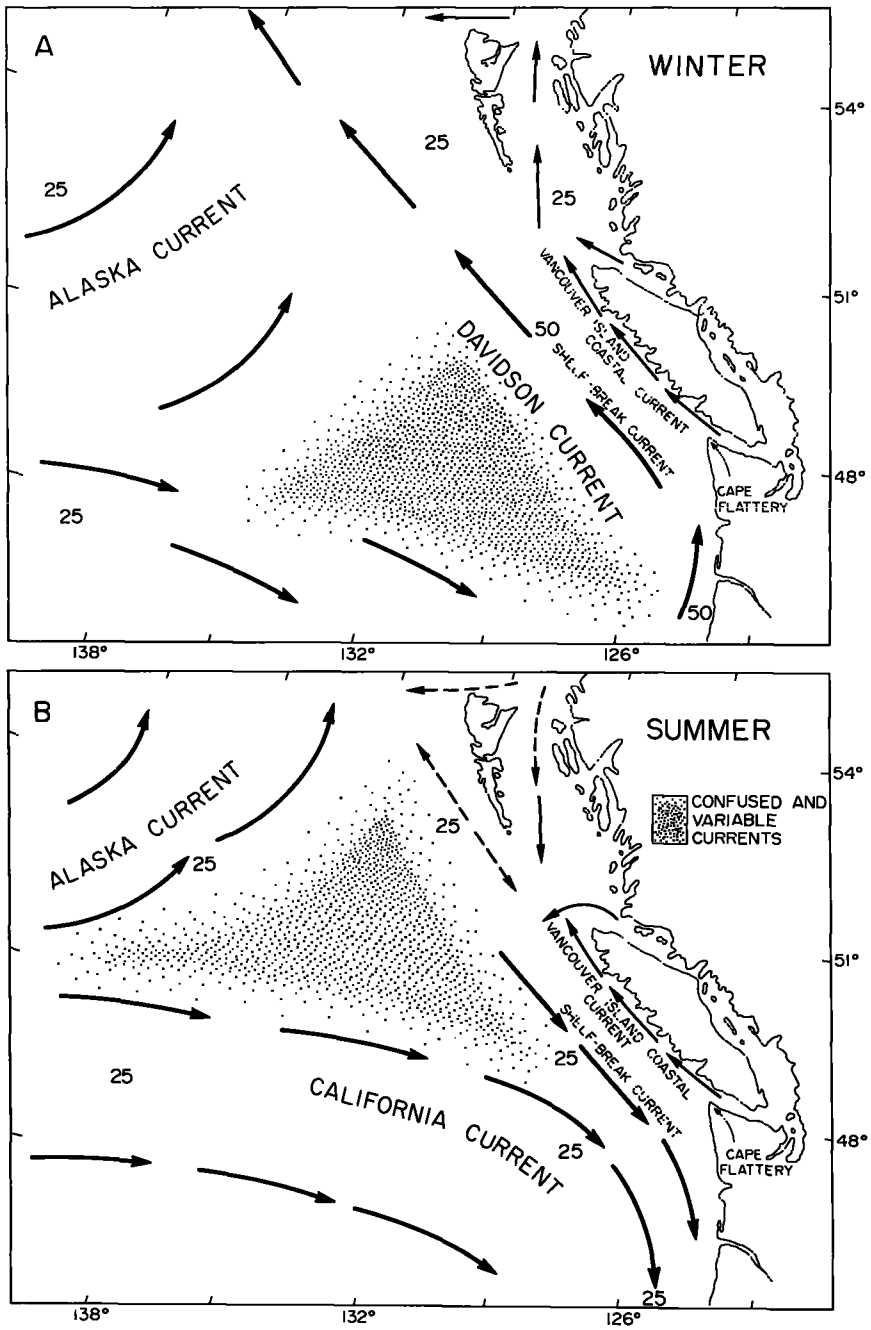

FIGURE 2.—Prevailing surface circulation off the British Columbia-Washington coast in winter and summer. Broken arrows indicate uncertain currents. Numbers give speeds (cm s^{-1}) (modified from Thomson 1981).

was the same size as that on the bongo gear. The neuston sampler was towed at 4 kn approximately 10 m from the side of the vessel to reduce hull avoidance by the larvae. Tow duration was usually 15 minutes but was shortened when crab larvae occasionally became very abundant at dawn and dusk.

Bongo gear was a modified SCOR design (Mason et al. 1984), having a mouth opening of 25 cm (each side) with the outboard (left) net of 500 μ Nitex and the inboard (right) net of 230 μ Nitex. A General Oceanics flowmeter was mounted in the mouth of each net. Sampling procedure followed that described by Smith and Richardson (1977[4]). At stations <100 m water depth, the bongo was fished in an undulating fashion from the bottom to the surface in order to filter a standard volume of water (about 300 m^3).

The epibenthic sled (Phillips and Mason 1986) used in inshore waters had a 60 cm mouth opening and 1 mm Nitex netting; it was towed for 10 minutes at 2–3 kn. Nine tows were made over bottoms of unknown characteristics. The modified beam trawl (Gunderson and Ellis 1986), also used in inshore waters, had a 3 m mouth opening, a 7 mm mesh net, and a 3 mm mesh cod end; it was towed for 10 minutes at about the same speed as the sled. For both gear types, distance towed was calculated by radar triangulation to reference points on land.

Data Analysis

All plankton samples were preserved initially in a 4% formaldehyde solution of saltwater. In the laboratory, settled volume was determined, and general composition of the plankton noted. Samples were then sieved, and *Cancer* larvae picked by hand and returned to a 2% formaldehyde solution before their identification. *Cancer magister* megalops are readily identifiable by their larger size (Trask 1970; Lough 1975), but the currently used key (Lough 1975) was not always effective in separating *C. oregonensis* and *C. productus*. Presence of lateral spines is a subjective criterion, and morphological dimensions and counts of setae were two variable to distinguish species. These smaller megalops were finally concluded to be *C. oregonensis* after rearing hundreds of larvae to the juvenile stage and finding no *C. productus*.

With beam trawl samples, the catch was sorted on deck to remove juvenile crabs, and the megalopae were preserved as above. Species composition of the catch was noted.

For the bongo tows, the volume of water filtered was used to calculate a haul factor (Mason et al. 1984), which accounted for tow depth and allowed expression of the data as the integrated number of organisms beneath 10 m^2 of sea surface.

For neuston tows, relative abundance was expressed as area swept rather than as volume filtered and again expressed as number of animals under 10 m^2 of sea surface.

Calculations of larval abundance are necessarily conservative, and direct comparisons between different gear types are not presently possible, given our current understanding of gear efficiency and larval catchability, which varies with both depth and time of day. Numbers of larvae reported here are thus directly comparable only within each gear type used. For bottom gear, numbers of crabs were calculated with no consideration of gear efficiency.

Molt Staging

State of development within the megalopal stage was determined for all *Cancer* megalopae collected at a station, or 25 randomly selected individuals of each species if the number collected exceeded 25. The sequence of epidermal changes occurring during this intermolt period has been described for Dungeness crab by Hatfield (1983), and her procedures and staging criteria were applied for both species. Whole megalopae were stained with 0.25% Fast Green dye in either water or polyvinyl lactophenol for 2–18 hours, and then the second maxillipeds were removed and mounted. Megalopae were identified to 1 of the 13 intermolt stages recognized by Hatfield (1983); these were then combined to form 3 groups: early (stages 1–4), middle (stages 5–8), and late (stages 9–13) megalopae. Temporal durations of these three groups in laboratory studies were 5.8, 15.4, and 6.3 days, respectively (Hatfield 1983). Corresponding durations for *C. oregonensis* are unknown. Stages were grouped into the three categories described for simplification of analysis; many of Hatfield's stages were of <48-h duration, and this was considered too fine a resolution for our purposes.

RESULTS

Water Temperature

Water temperature at the surface ranged from

[4]Smith, P. R., and S. L. Richardson. 1977. Manual of methods for fisheries resource survey and appraisal. Part 4. Standard techniques for pelagic fish egg and larval surveys. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Adm. Rep. No. 77-11.

8.4° to 14.4°C, and from 7.6° to 8.8°C at 50 m, during the period 17 April to 7 July (Table 1). Warmest surface temperatures were in May and July, and at 50 m, were warmest in June.

Species Occurrence

Three species of crab larvae predominated in the plankton collected. The porcellanid crab, *Petrolisthes cinctipes*, predominated in waters within 8 km of shore, while *C. oregonensis* and *C. magister* dominated in more offshore waters. Other crab species were present but at much lower abundance than these three species. Megalopae of *C. oregonensis* were of comparable abundance to *C. magister* at most stations sampled.

Surface Abundance

Presence of crab megalopae at the surface was dependent on time of day, with slight differences in timing of maximal abundance occurring between the two *Cancer* species (Fig. 3). At 9.3 km offshore in June, *C. oregonensis* was several orders of magnitude more abundant and also seemed to peak in abundance a little earlier in the evening and later in the morning than did *C. magister*. Relative abundance of both species declined in the middle of the night.

Data in Figure 3 was smoothed by eye (Fig. 4) to allow megalopal abundance data from the transect to be weighted by time of capture at night. Multiplier values were determined, and these were used to adjust actual abundance data by sampling time for the May and June sampling periods (Tables 2, 3). Only these data were weighted, and since day length changes with time of year, adjustment of data collected more than two weeks on either side of 14 and 15 June was considered inappropriate.

In hindsight, some data (indicated by asterisks in Tables 2, 3) was found to have been collected at a time when megalopae were just beginning to reach, or had just left, the surface. The calibration slope (Fig. 4) is very steep at both these times and it was impossible to estimate accurately a meaningful scaling multiplier for these data. Our estimated megalopal abundance at these stations should be viewed with particular caution; a zero value may not indicate that megalopae were absent, but only that they were not at the surface.

Bongo tows during the day poorly sampled the abundance of *C. magister* megalopae (Table 4) shown to be present by nighttime neuston tows (Tables 2, 3). This was possibly due to sampling the total column below only a few square meters of sea surface, because of integration of the results, or to avoiding the net by the megalopae. It was unlikely because of failure to sample deeply enough, since on the continental shelf, tow depth approached bottom depth. Megalopae (maximum per tow was 4) were primarily collected by bongo gear at stations where they were abundant in neuston samples at night, but relative abundance estimates obtained from bongo nets are considered only useful in a general qualitative sense because of the low absolute numbers caught.

Temporal Occurrence (Time of Year)

No *Cancer* megalopae were found in samples collected shortly after dusk on 27 February–4 March. *Cancer* megalopae were first observed on the next

TABLE 1.—Water temperatures (°C) by depth (m) at the stations sampled off Tofino, B.C. on 17 April, 31 May, 14 June, and 6 and 7 July 1985.

Distance offshore (km)	Depth (m)											
	April			May			June			July		
	0	20	50	0	20	50	0	20	50	0	20	50
0	8.8	8.8		12.2	9.2		12.2	11.4		—		
9	8.8	8.7		13.4	9.5		12.2	9.0		13.5	11.0	
19	8.7	8.1	7.9	13.4	8.6	7.6	12.3	10.4	8.0	14.0	9.0	7.6
28	8.8	8.8	8.2	13.1	9.6	7.9	12.8	12.3	8.0	13.3	10.0	7.7
37	8.6	8.6	8.3	13.8	9.3	7.9	12.7	9.4	8.3	13.3	10.7	7.7
56	8.7	8.7	8.2	13.3	9.8	8.2	12.9	10.5	8.1	14.4	13.3	8.6
74	8.7	8.6	8.2	11.8	10.0	8.2	12.9	12.0	8.7	14.4	13.3	8.6
93	8.5	8.5	8.2	11.9	10.3	8.2	12.8	12.2	8.5	—	—	
111	8.5	8.4	8.0	11.5	10.5	8.1	12.7	12.2	8.5	—	—	
130	—	—	—	—	—		12.7	12.4	8.6	—	—	
148	8.5	8.5	8.0	11.0	10.0	8.7	—	—	—	—	—	
165	8.4	8.6	8.4	11.4	10.0	8.4	—	—	—	—	—	

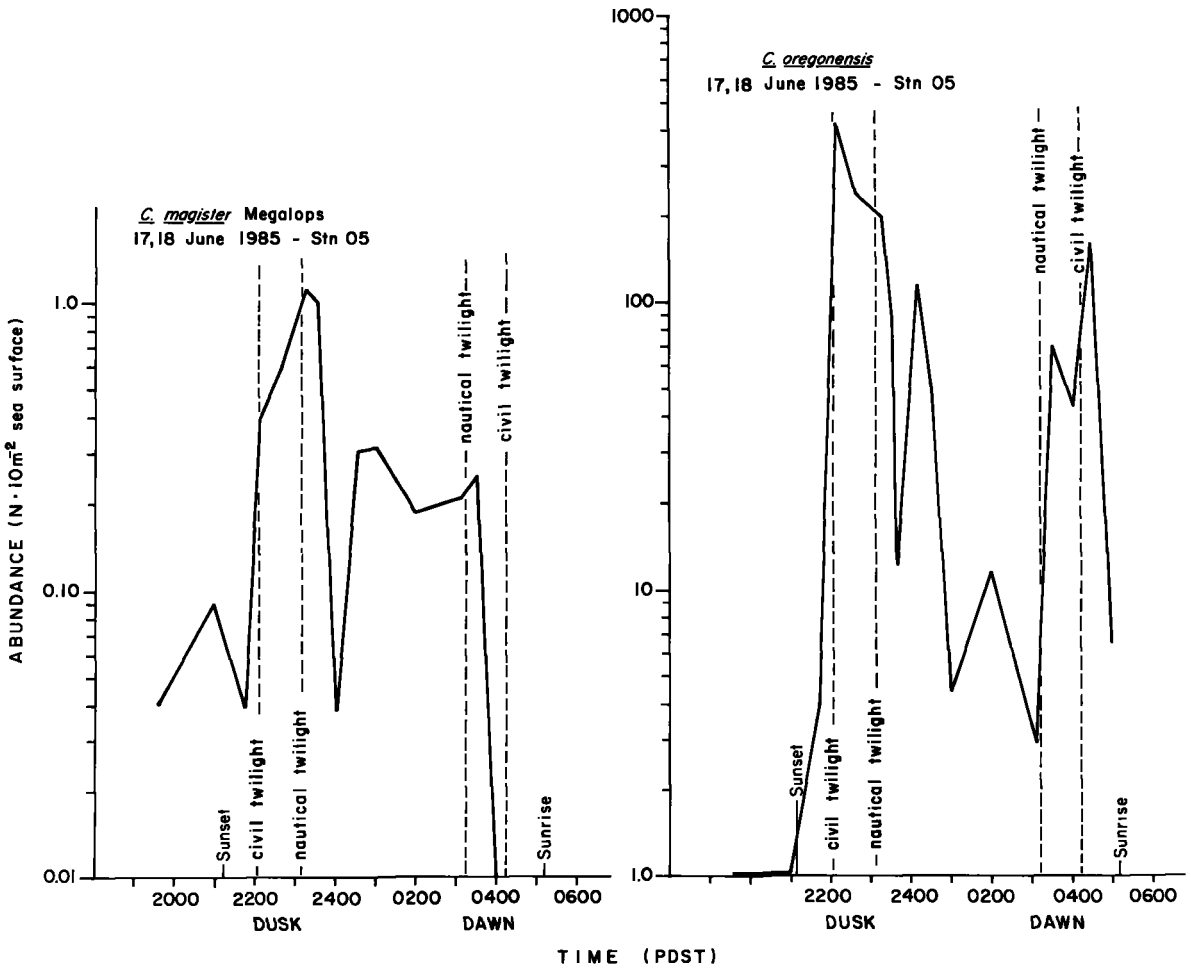

FIGURE 3.—Neustonic abundance of *Cancer magister* and *C. oregonensis* megalopae observed during sampling through one night at a station 9 km off the coast off Tofino, B.C.

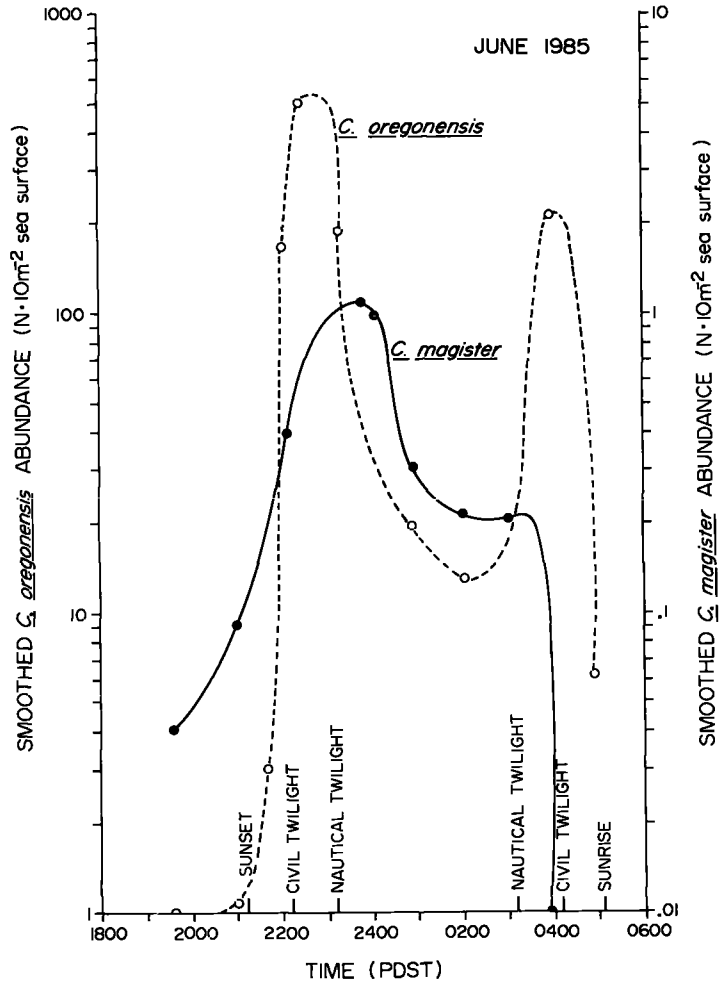

FIGURE 4.—Smoothed abundance of *Cancer magister* and *C. oregonensis* megalopae observed during sampling through one night at a station 9 km off the coast off Tofino, B.C.

TABLE 2.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 30 and 31 May 1985. * = Value uncertain because of time of sampling. Values rounded to one decimal place.

Time	Distance (km)	*C. magister* (N 10 m^{-2}) Multiplier	Unscaled	Scaled	*C. oregonensis* (N 10 m^{-2}) Multiplier	Unscaled	Scaled
18:12	0	∞	2.3	?*	∞	0	0*
19:02	9	36.7	0.2	7.2*	∞	4	?*
19:43	19	26.8	0.0	1.1*	∞	0	0*
20:26	28	20.0	0	0	∞	0	0*
21:09	37	11.0	0.4	4.7	∞	0	0*
21:52	46	3.9	14.4	56.4	5.2	2.2	11.5
22:35	56	1.6	29.9	47.0	1.0	0.1	0.1
23:37	74	1.0	17.0	17.0	—	0	0
00:47	93	3.3	36.0	119.9	24.8	1.0	25.7
01:55	111	5.0	2.6	13.3	40.0	1.8	72.1
03:56	148	110.0	1.1	118.4*	2.5	0.1	0.2
05:57	185	∞	0	0*	∞	0	0*

sampling date, 16 and 17 April, but maximum abundance (unweighted as to diel time of sampling) occurred in late May and the second week of June (Fig. 5). *Cancer magister* megalopae were collected as late as 24 August, the last sampling date, but relative abundance along the transect was low after the beginning of July.

Cancer oregonensis megalopae were caught in April but occurred in abundance only in the late May and mid-June surveys, with peak abundance in June.

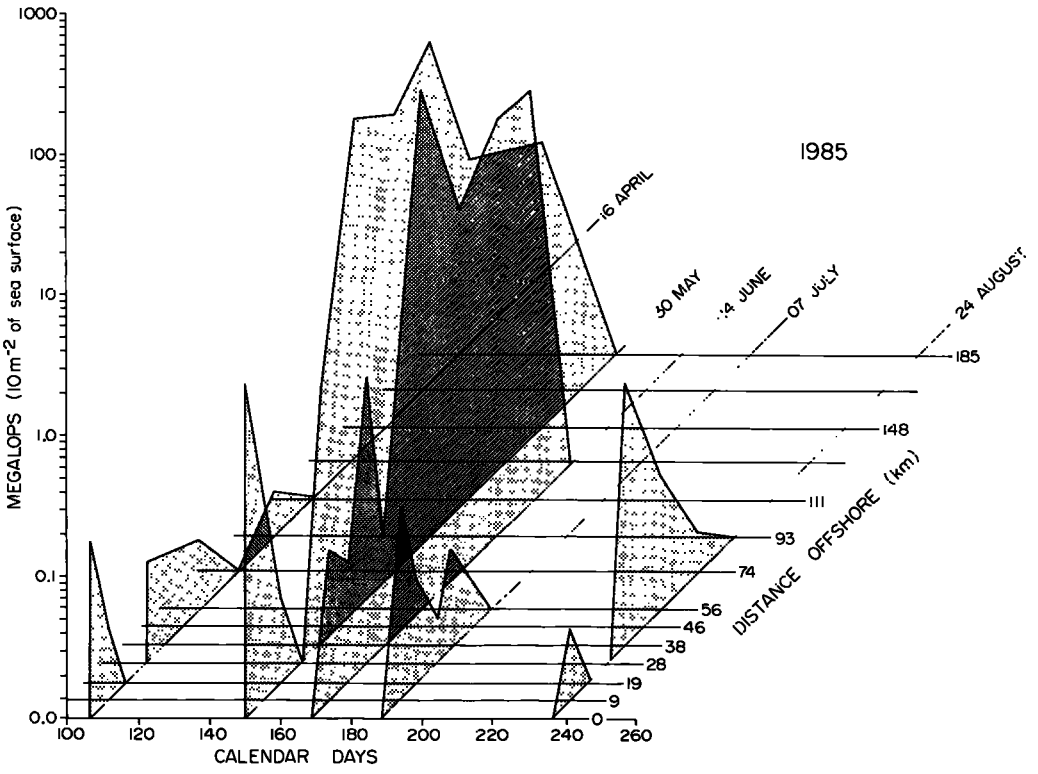

FIGURE 5.—Neustonic abundance of megalopae observed along the transect line during April to August 1985 surveys.

TABLE 3.—Scaling values used to standardize the actual number of megalopae caught (unscaled) to the estimated number which would have been caught at the times of peak nocturnal abundance, 22:40 and 23:40 hours, for *Cancer oregonensis* and *C. magister*, respectively, on 14 and 15 June 1985. * = Value uncertain because of time of sampling. Values rounded to one decimal place.

Time	Distance (km)	*C. magister* (N 10 m^{-2})			*C. oregonensis* (N 10 m^{-2})		
		Multiplier	Unscaled	Scaled	Multiplier	Unscaled	Scaled
01:42	0	—	0	0	37.1	8.8	327
00:58	9	3.6	0.1	0.4	27.4	170.5	4,671
00:09	19	1.2	0.1	0.1	16.3	0.1	2.3
23:19	28	1.0	0.2	0.2	2.7	7.6	20.5
05:36	37	∞	0.1	?*	∞	0	0*
03:52	56	55.0	52.2	2,871*	2.6	15.7	40.9
02:02	74	5.2	3.7	19.2	40.0	4.8	192
00:25	93	2.4	8.9	21.6	20.8	1.5	30.4
22:45	111	1.2	8.4	10.3	1.0	12.5	12.5
21:10	130	—	0	0	—	0	0

TABLE 4.—Tow characteristics and number of *Cancer magister* megalopae (10 m^{-2} of sea surface) caught by 0.25 m^2 bongo tows off Tofino, B.C., on 31 May and 14 June 1985.

	May					June				
Distance offshore (km)	Time (h)	Water volume (m^3)	Max. depth (m)	No. megalops	Megalopae (N 10 m^{-2})	Time (h)	Water volume (m^3)	Max. depth (m)	No. megalops	Megalopae (N 10 m^{-2})
0	19:27	210	33	1	1.6	08:00	240	36	3	4.5
9	18:52	182	55	1	3.0	08:55	220	55	0	0
19	18:16	114	72	0	0	09:51	222	75	0	0
28	17:37	166	120	0	0	10:50	209	115	0	0
37	16:55	199	151	0	0	11:47	284	146	1	5.1
56	15:30	352	250	4	28.4	13:32	381	192	0	0
74	14:07	327	250	1	7.6	15:21	338	200	1	5.9
93	12:42	326	250	3	23.0	17:04	296	200	2	13.5
111	11:17	360	250	1	6.9	18:56	269	200	0	0
130	—					21:12	327	200	2	12.2
148	08:55	400	250	0	0	—				
185	06:18	319	250	0	0	—				

Cross-Shelf Spatial Distribution

With both species, no clear pattern in cross-shelf distribution was evident from the April data, perhaps because of relatively low overall megalopal abundance. In late May (Table 2), scaled abundance (weighted as to time of night) of *C. magister* was highest at 93 km offshore, but megalopae were generally abundant (>10 10 m^{-2} sea surface) from 46 to 148 km offshore. In mid-June, the basic pattern observed in late May was still evident, although megalopal abundance near shore had declined (Table 3). Highest estimated *C. magister* abundance was at 56 km offshore.

With *C. oregonensis*, scaled abundance in late May peaked (>20 10 m^{-2}) 93–111 km offshore (Table 2). An exceptionally large number of megalopae (4,671 10 m^{-2}) was found 9 km offshore in June (Table 3), while from 56 to 111 km offshore, abundance remained high (>20 10 m^{-2}).

Sampling of inlet waters around Tofino with neuston gear showed that a few *Cancer* megalopae were present but that no substantial (average was <1 10 m^{-2}) numbers occurred. Maximum *C. magister* megalopal abundance was 2.9 megalopae 10 m^{-2} on 5 June, with megalopae observed only between 29 May and 19 June. Maximum *C. oregonensis* abundance was 2.3 megalopae 10 m^{-2} on June 19, with megalopae observed only between 4 and 19 June.

Intermolt Stage

All *C. magister* megalopae collected in April were of early developmental stage (Fig. 6), whereas all those collected in August were mid-stage megalopae. In May, June, and July, the general pattern of offshore distribution by molt stage was for late stage larvae to be nearest inshore and early stage larvae to be furthest offshore.

Cancer oregonensis megalopae had a similar developmental distribution pattern to those of *C. magister* (Fig. 7); late molt megalopae were most abundant closest to shore. However, in late May, most megalopae were early stage, in contrast to *C. magister*, whereas by mid-June, all three intermolt groups were present.

When the scaled megalopal abundance at distance offshore (Tables 2, 3) is multiplied by the percentage at each molt stage at a specific location (Figures 6, 7, for each species, respectively), the actual abundance by molt group with distance offshore is determined (Figures 8, 9, respectively). In late May, late stage *C. magister* megalopae were relatively abundant 9 km offshore, indicating that some Dungeness crab settlement may have occurred. However, larval sampling in the inlets and bays showed few megalopae present. In contrast to previous years, no recently settled juvenile crabs (0 age-class crabs) were found by local fishermen in intertidal areas or on floating objects, confirming that the magnitude of megalopal settlement in 1985 was relatively small. In mid-June, there were few *C. magister* megalopae of any intermolt stage present within 40 km of the coast and little evidence of late stage megalopae offshore. Early and mid-stage megalopae were most abundant from 56 to 111 km offshore.

For *C. oregonensis*, the opposite was observed (Fig. 9). Few late stage megalopae were present in late May, and unlike *C. magister*, megalopae were not concentrated in nearshore waters. However, megalopae in all three intermolt stages were abundant inshore in mid-June, with late stage megalopae dominating at the coast. The timing of occurrence

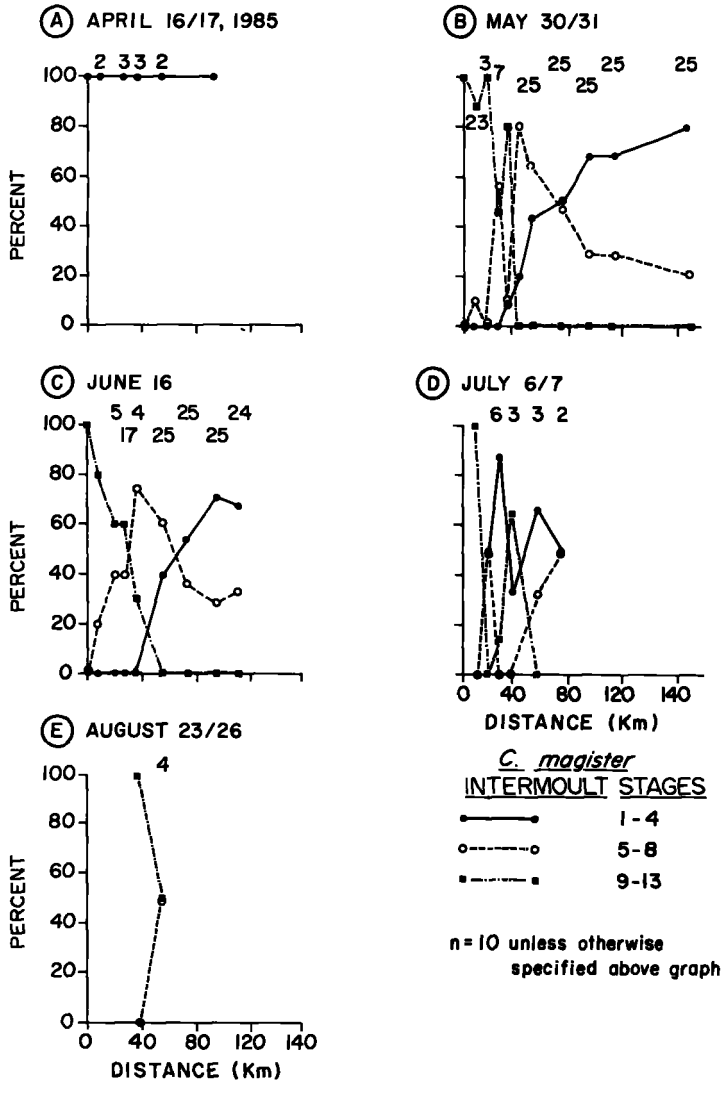

FIGURE 6.—Percentage of the three *Cancer magister* megalopal intermolt groups observed at each station during the April to August 1985 surveys.

of late stage megalopae at the coast thus differed between the two species.

Inshore Benthic Sampling

Survey of commercial crab habitat with beam trawls and an epibenthic sled yielded few newly settled megalopae or juvenile *C. magister* (Table 5). A maximum of 83 crab/10,000 m^2 was collected, well below densities which might be expected if settlement had been substantial. No *C. oregonensis* were caught, perhaps because of the habitat being sampled, and no larval settlement of either species was observed when intertidal mud flat areas were searched by foot. In a concurrent study, no significant abundance of 0 age-class *C. magister* was observed during monthly sampling throughout the remainder of the year.

DISCUSSION

Megalopal Source

Temporal duration of *C. magister* larval stages has been estimated both by laboratory rearing (Poole 1966; Reed 1969; Brugman 1972; Gaumer 1973; Ebert et al. 1983) and the first appearances of larval stages in field studies (Poole 1966; Lough 1976; Reilly 1983). The length of the total larval period has been estimated as 105–125 days by Reilly (1983),

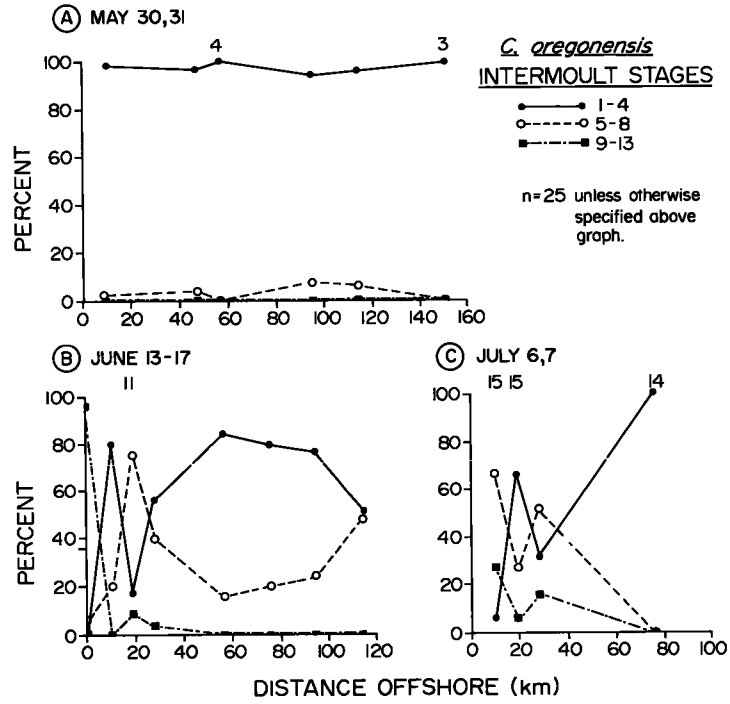

FIGURE 7.—Percentage of the three *Cancer oregonensis* megalopal intermolt groups observed at each station during the May to July 1985 surveys.

TABLE 5.—Beam trawl and epibenthic sled catches from nearshore waters around Tofino, 16–18 June 1985.

Area	Depth (m)	Gear type	Area swept (m^2)	Catch of crabs		No. 10^4 m^{-2}	
				Juveniles	Megalops	Juveniles	Megalops
Templar Channel	7	trawl	2,650	5	0	26	0
		sled	375	0	0	0	0
Chesterman Beach	5	trawl	—	—	—	—	—
		sled	300	0	0	0	0
Cox Bay	8	trawl	2,500	1	0	4	0
	7	sled	400	3	0	75	0
	13	trawl	2,600	7	0	27	0
	15	sled	420	2	0	48	0
	30	trawl	2,260	0	0	0	0
	23	sled	360	0	3	0	83
Lennard Island	25	trawl	—	—	—	—	—
		sled	350	0	0	0	0
Long Beach	7	trawl	2,700	5	0	18	0
		sled	400	2	0	50	0
	13	trawl	2,650	6	1	23	4
		sled	400	2	1	50	25
	23	trawl	—	—	—	—	—
		sled	220	0	1	0	45

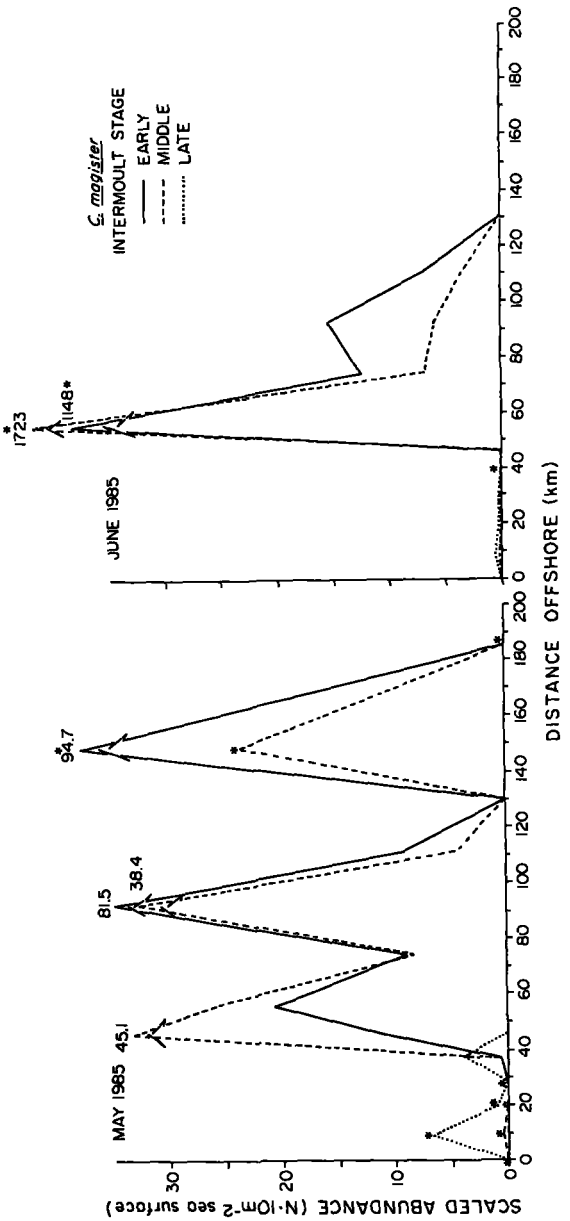

FIGURE 8.—Scaled abundance of *Cancer magister* megalopae by intermolt group observed at each station during the May and June 1985 surveys.
* = Value uncertain because of time of sampling.

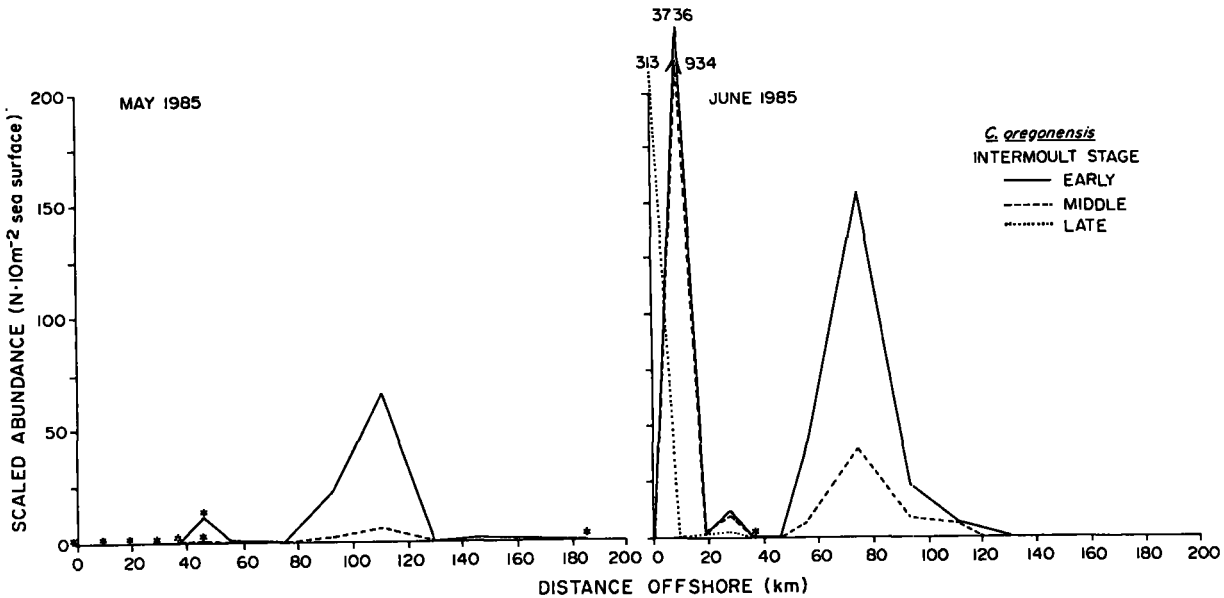

FIGURE 9.—Scaled abundance of *C. oregonensis* megalopae by intermolt group observed at each station during the May and June 1985 surveys.
* = Value uncertain because of time of sampling.

130 days (range: 89–143) by Lough (1976), 45 and 108 days at 17.8° and 10.0°C, respectively, by Reed (1969), and 128–158 days under natural conditions by Poole (1966). In laboratory studies, Poole (1966) found the total time required was 111 days at 10.5°C. Since water temperatures typically range from about 8° to 13°C off the British Columbia-California coast during January-February (Thomson 1981), the total larval period in the study area is assumed to be about 110 days.

Off Vancouver Island, megalopae can be collected in abundance in open coast waters from mid-April to August. Ovigerous Dungeness crab, collected at Tofino and held in ambient temperature seawater at Nanaimo, hatched their eggs from January to March, with most hatching occurring in February (G. Jamieson, unpub. data). This suggests that megalopae collected between April and June could be from local populations whereas most megalopae collected in July and August may have largely originated elsewhere.

Lough (1975) stated that the hatching period of *C. oregonensis* off Oregon extends from January to July, with two broods indicated, one primarily hatching in February and the other in May–June. He estimated larval duration of a brood at 155 days (range: 123–203 days) from field sampling, but there was possible intermixing of the larvae from different broods, as well as population variability in the timing of hatching. We have no data on the hatching period of this species in British Columbia.

Given the currents off the west coast of Vancouver Island, then, *Cancer* larvae present there in the spring could theoretically have originated anywhere between northern California to perhaps southern Alaska. It seems very unlikely that the larvae are entirely the progeny of adult crabs on the west coast of Vancouver Island.

Onshore Movement

Geographical location of larval settlement is very dependent on currents. Adult *Cancer* of both species are largely found in nearshore, shallow-water habitats (Hart 1982), and such environments are apparently both the origin and preferred destination of larval crabs (Butler 1956). Along the open coast, Dungeness crab larvae are known to settle in both estuarine and nearshore areas (Wild and Tasto 1983; Stevens and Armstrong 1984; Armstrong and Gunderson 1985). In waters largely surrounded by land, such as Puget Sound, Georgia and Queen Charlotte Straits, and, to a lesser extent, Hecate Strait, Dixon Entrance, and southeastern Alaska, larval crabs may perhaps remain nearshore throughout their entire developmental period. However, studies suggest that while larvae may be hatched nearshore along the outer coast, they subsequently move offshore and then inshore (Lough 1976; Reilly 1983). The extent to which this may occur can profoundly affect the degree of dispersal of a local region's progeny.

Evidence for an offshore-onshore movement of *C. magister* during the larval development period is ambiguous. In the field, three studies of the offshore spatial pattern of larval distribution have been undertaken: off central and northern California (Reilly 1983), off Newport, Oregon (Lough 1976), and off Tofino, British Columbia (this study). The California study extended to about 185 km from shore from San Francisco north to Cape Mendocino, with some earlier CALCOFI data (1949–75) extending to about 275 km offshore included. Sampling consisted of discrete-depth and oblique plankton tows and was mostly during the day. The sampling gear (0.5 m diameter opening) most often used was preceded by the towing cable and bridle (P. Reilly[5]), and gear avoidence by same megalopae may have occurred. Because of the gear and protocol used, it is difficult to interpret Reilly's (1983) results in a quantitative sense. However, offshore movement of larvae during zoeal stages II–V was indicated, as was the later presence of megalopae in nearshore waters following a period when stage V zoeae were generally absent from within 40 km of shore, but a mechanism to explain the onshore transport of megalopae was not established. As part of the overall study (Wild and Tasto 1983), Hatfield (1983) determined the intermolt stage of many larvae collected by Reilly (1983). Earlier stage megalopae were in general collected further offshore, earlier in the year, and at a lower latitude.

The Oregon study (Lough 1976) was on one trackline extending 110 km offshore off Newport, with mostly daytime, oblique bongo samples collected at specified stations. Although early stage zoeae of both species were abundant nearshore, late stage zoeae were not, and were largely collected at the offshore stations. Lough (1975) noted that *C. oregonensis* megalopae were found further offshore and later during the summer upwelling season than were *C. magister* megalopae. In 1970, large numbers of *C. magister* megalopae, which were not intermolt staged, were found inshore. In 1971, virtually no *C. magister* larvae older than stage III were collected

[5]P. Reilly, California Department of Fish and Game, Menlo Park, CA 94025, pers. commun. February 1988.

at any of the stations, and Lough suggested that a mass mortality of *C. magister* larvae might have occurred. In contrast, *C. oregonensis* larvae were in greater abundance during 1971 than 1970.

Results from the current study and Booth et al. (1985) suggest that the sampling gear and procedures used by Reilly (1983) and Lough (1976) gave poor abundance estimates of megalopae. The number of megalopae caught during daylight is relatively low, and the presence or absence of only a few megalopae can greatly influence the estimated megalopal density per unit of sea surface. This sensitivity to bias can only be compensated for by many replicate samplings, and it is logistically easier to estimate absolute megalopal abundance by sampling at night when megalopae are concentrated in a relatively easily sampled, narrow depth range, namely the neuston (Booth et al. 1985). Reilly (1983) sampled once both day and night at 12 stations, and noted no significant differences in megalopal density between day and night at the surface and in oblique tows. However, his surface tows were not neuston tows, and consisted of a 0.5 m diameter net towed about 0.25–0.5 m below the water surface, or below the wave troughs if the surface was rough (P. Reilly fn. 5). This qualifies his observations, and may explain the suggested low abundance of megalopae in his study area (maximum density was 43 100 m^{-3} at the surface).

On occasion, megalopae have been observed to be in association with *Velella velella* at the surface during daylight (Wickham 1979; Reilly 1983; G. Jamieson unpub. data), but we have generally observed relatively few megalopae in surface waters during the day in comparison to the number observed present at night. Accepting that relative megalopal abundance is best determined at night from neuston tows, megalopae off British Columbia were shown to be abundant in specific areas offshore and at these locations, early and mid-stage megalopae predominated.

All three studies indicate that 1) later stage *C. magister* larvae are found offshore and, since they are hatched at inshore locations, some mechanism must be transporting them away from shore, 2) megalopae are found inshore, with Hatfield (1983) and this study showing that earlier stage megalopae predominate furthest offshore, and 3) while longshore drift of larvae may occur, it is difficult to establish its significance in the absence of simultaneous current and larval distribution data, both geographically and vertically in the water column. None of these studies demonstrates conclusively that larvae which ultimately settle inshore were ever very far offshore, and while it is shown that larvae can be carried offshore in abundance, this may well represent larval wastage, in that relatively few of them, if any, may ultimately return inshore to survive at settlement. The same is assumed to apply for *C. oregonensis*.

The California data on larval distribution, which is the most extensive spatially, are somewhat ambigious in that they may be interpreted either as onshore-offshore-onshore movement, or as a general offshore dispersal coupled with northwards-southwards drift of those larvae remaining inshore. To account for an absence of middle stage larvae in the nearshore waters of Reilly's (1983) study area, the latter scenario assumes that larval crab production south of the Gulf of the Farallones is relatively low, and that the water mass entering the sample area from the south as part of the Davidson Current contains few larvae. Little data appear to exist to refute this possibility; the commercial fishery for Dungeness crab only exists at a few locations south of San Francisco, and then only sporadically (Warner 1985). Our data and Lough's (1976) data are inadequate to investigate longshore drift because biological samples in each study were only collected along one offshore transect and no data on currents was simultaneously obtained.

Off the west coast of Vancouver Island, we found that megalopae may be concentrated in areas between surface currents flowing in opposite directions, specifically in the shear between the Vancouver Island Coastal Current and the outer Shelf-Break Current. Megalopae were abundant 40–70 km from shore, with *C. magister* megalopae particularly concentrated about 50 km from shore. In 1985, there was no major crab settlement observed on the outer coast near Tofino, suggesting that the Coastal Current may sometimes be an effective barrier to onshore movement and successful settlement. Understanding the horizontal and vertical distributions of crab larvae in the water column now seems essential if transport mechanisms of larvae and their movement from hatching to settlement are to be understood.

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FOOD PATHWAYS ASSOCIATED WITH PENAEID SHRIMPS IN A MANGROVE-FRINGED ESTUARY

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ABSTRACT

High abundance and production of juvenile *Penaeus* spp. in tropical estuaries has been attributed to high concentrations of mangrove-derived detritus in the nursery habitats. Examination of the diets of *Penaeus notialis*, *P. subtilis*, and *P. brasiliensis* in the mangrove-fringed Laguna Joyuda, Puerto Rico showed that even the smallest juveniles are predators consuming capitellid polychaetes (20–38% of diets) and amphipods (20–76%). Less than 25% of the diets was detritus. Ontogenetic variation in diets was greater than interspecific variation, and there was no evidence for dietary separation among the sympatric species. Seasonal shifts in foods reflected abundance patterns of macrobenthic prey species. Despite the consumption of prey organisms generally classified as detritivorous, stable carbon isotope ratios in the penaeids (−18.1 to −15.0‰), their food items (−18.8 to −17.7‰), and primary producers indicated that shrimps and the majority of sediment dwellers in Laguna Joyuda obtain most of their carbon from benthic algae (−14.4‰) and not from mangrove detritus (−25.0 to −22.9‰).

The juveniles of penaeid shrimps are abundant in many tropical and subtropical estuaries of the world, particularly where wetland habitats such as marsh grasses or mangroves are prominent coastal features (Edwards 1978; Staples 1980; Stoner 1988). The relationship between wetlands and commercial shrimp has been attributed to at least two factors: high food abundance and shelter from predators, the relative importance of which is still debated (Boesch and Turner 1984). Early wetland studies (Odum and Heald 1972, 1975) suggested that a large variety of fishes and invertebrates including *Penaeus* spp. were directly dependent upon detritus from the vascular wetland plants. More specific studies of penaeid diets have since revealed that the shrimps are omnivorous or carnivorous in many shallow-water habitats (Moriarty 1976, 1977; Chong and Sasekumar 1981; Moriarty and Barclay 1981) and that some species may have a direct influence on the abundance of small macrofauna (Leber 1983, 1985).

The most important commercial shrimp species in the Caribbean Sea and along the north coast of South America are *Penaeus notialis*, *P. subtilis*, *P. brasiliensis*, and *P. schmitti*, all of which have nurseries in coastal wetland habitats (Stoner 1988). Although the biology of tropical Atlantic penaeids has been studied in a few localities (Neiva 1969; Nikolic and Ruiz 1969; Lindner 1971; Garcia 1974; Garcia et al. 1985), we have found no information on their diets.

Examinations of shrimp diets reported here were conducted in a small coastal lagoon in Puerto Rico where *Penaeus* populations are large and where four species coexist (Stoner 1988). In this report, diets of the three most abundant *Penaeus* species are described with particular reference to ontogenetic variation, similarities among the species, the significance of detritus, and seasonality in diets as related to the abundance of foods in the field.

Because foods are retained and assimilated differentially in the gut, examination of gut contents does not necessarily give a true indication of the relative importance of foods. For example, detritus has been reported as a significant component of the gut contents of *Penaeus* spp. (Odum and Heald 1972), but detritus is known to be indigestible compared with soft-bodied prey organisms such as polychaetes. Furthermore, in the case of predators, the primary source of carbon is not revealed through gut analysis. For these reasons, stable carbon isotope ratios were measured for *Penaeus* spp. and most other organisms common in the lagoon.

METHODS AND MATERIALS

Shrimps were collected in Laguna Joyuda on the west coast of Puerto Rico (lat. 18°07'N, long.

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67°11'W). The study site and shrimp and fish populations in the lagoon have been described by Stoner (1986, 1988). Briefly, Laguna Joyuda is a polyhaline basin with a total surface area of 1.21 km^2 and an average depth of approximately 1.5 m. One narrow channel 0.5 km long represents the only connection to the Puerto Rico shelf. Lagoon sediments are mostly fine mud and sand with very high organic content derived from red, white, and black mangroves which surround approximately 75% of the shoreline. Over the last 20 years the lagoon has had a salinity range of 4 to 44‰, depending upon precipitation and degree of channel closure (A. W. Stoner, unpubl. data).

Four penaeids utilize the lagoon as a nursery area. *Penaeus notialis* and *P. subtilis* are approximately equal in abundance and together comprise over 92% of the total penaeid assemblage (Stoner 1988). *Penaeus brasiliensis* made up 7.0% of the total collection in 1984 to 1985, and *P. schmitti* was relatively uncommon, making up <0.3% of the total (Table 1). For this study, we examined the diets of the three most abundant shrimp species.

Penaeids were collected with a 5 m otter trawl with 2.5 cm wings and body, and 5 mm cod end liner. All collections were made between nautical twilight and midnight at three sites: a northern muddy bottom arm of the lagoon (station 5), a sandy mud site in the central basin (station 3), and a sandy mud site near the channel (station 1). Collections were made monthly, during the last quarter of the moon, from July 1985 to June 1986.

Shrimps were divided into size classes on the basis of carapace length (CL) for gut content analyses. Penaeid shrimps between 3 and 6 mm CL could not be identified to species and were simply identified as *Penaeus* juveniles (all were of the grooved variety and, therefore, did not include *P. schmitti*). Shrimps larger than 6 mm CL could be identified and were examined by individual species in 4 mm size classes, up to 26 mm CL in the case of *P. subtilis*. To yield sufficient numbers of individuals in all size classes for each monthly collection, members of individual species were pooled from all sampling areas. In the case of *P. brasiliensis*, collections from 2-mo intervals were pooled to analyze seasonal variation in the diets of this less abundant species. Food items taken from the proventriculus of up to 25 shrimp were pooled for each sampling date and size class, and preserved with 70% isopropanol and a dilute solution of rose bengal stain.

We used the gravimetric sieve fractionation procedure developed by Carr and Adams (1972) to analyze gut contents of the shrimp. This procedure has been widely used for juvenile fishes (Sheridan 1979; Stoner 1980; Livingston 1984) and a variety of decapod crustaceans, including *Penaeus* spp. (Laughlin 1982; Leber 1983). Gut contents were washed through a series of six sieves of decreasing mesh size (2.0–0.075 mm mesh) and each sieve fraction was examined with a dissecting microscope. Because all of the items in a particular sieve fraction were of approximately equal size, the relative proportion of the gut contents made up of each food type was measured directly by counting. After examination, each sieve fraction was dried overnight at 80°C and the total contribution of each food type to total dry weight was calculated.

With few exceptions, each food particle was placed in a mutually exclusive category (Table 2). In most cases, food items or fragments could be identified to major taxonomic group such as Amphipod or Polychaete. The classification "Animal Remains" was applied where fragments were unidentifiable to taxon, but where the tissue was stained by rose bengal. The major food categories were used for statistical interpretation of diets; however, whenever an animal or plant could be identified to a lower taxonomic level, this information was recorded.

Similarities between and among the diets of various shrimp species and size classes were measured with Czekanowski's coefficient (Bray and Curtis 1957; Field and McFarlane 1968). Dendo-

TABLE 1.—Composition of the penaeid shrimp assemblage at three stations in Laguna Joyuda, Puerto Rico, during the 12-mo study period. Values are total numbers collected in 72 trawl samples and percentages of totals at the individual sites (parentheses).

Species	Station 1	Station 2	Station 3
Penaeus notialis	282 (49.1)	271 (53.6)	229 (48.6)
P. subtilis	236 (41.1)	185 (36.5)	217 (46.1)
P. brasiliensis	54 (9.4)	50 (9.9)	22 (4.7)
P. schmitti	2 (0.4)	0 (0)	3 (0.6)
Totals	574	506	471

TABLE 2.—List of the general food categories encountered in the foreguts of *Penaeus* species and the codes employed in histograms for shrimp diets.

AM	Amphipod	OS	Ostracod
CC	Calanoid copepod	PM	Plant material (green)
CY	Cyclopoid copepod	PO	Polychaete
CZ	Crab zoea	RU	*Ruppia maritimia*
DE	Detritus	SA	Sand
FO	Foraminifera	TA	Tanaidacean
FR	Fish remains	TH	*Thalassia testudinum*
HC	Harpacticoid copepod		
GA	Gastropod	MS	Miscellaneous—used in histograms for all food items making up <4% of the total dry weight.
IE	Invertebrate egg		
NE	Nematode		

grams were then constructed by complete linkage classification.

Plant and animal materials were collected from the lagoon for stable carbon isotope analyses on several occasions between 1981 and 1984. These were taken to give an indication of the range of $\delta^{13}C$ values between organisms associated with mangroves, plankton, and benthos and to test the efficiency of using the technique to identify food pathways. Materials were collected with trawl, sieve, plankton net, and by hand. All materials were fresh and not exposed to chemical preservatives. In the field, samples were placed in plastic bags on ice as temporary storage. Within 24 hours, these samples were flushed free of salt using deionized water, dissected to acquire tissue uncontaminated by gut contents and outside shells, treated for 5 to 10 minutes with 5% phosphoric acid to remove carbonates, double rinsed in deionized water, and oven-dried at 70°C until brittle. Dried samples were ground to a fine powder with a mortar and pestle, packaged in plastic bags, labeled, and stored for later mass spectrometer analyses. The homogenized samples were combusted at 550°C for 24 hours in the presence of CuO in evacuated sealed pyrex tubes using techniques modified from Stofer (1980). CO_2 gas was analyzed from the combusted samples on a Finnigan - MAT 251[3] isotope ratio mass spectrometer. $\delta^{13}C$ was calculated according to Craig (1957) and methods and definitions generally followed those reviewed by Fry and Sherr (1984). For small animals and all plants, the entire organism (with guts removed where possible) was used in analyses. For large animals, muscle tissue was removed from the body and used separately for analyses. In most cases, organisms were pooled to acquire mean $\delta^{13}C$ values for n individuals. Unlike more complex marine systems (Fry et al. 1982), our $\delta^{13}C$ were well separated between groups of species and distinctions were relatively clear-cut. Since diversity was also relatively low in the lagoon, $\delta^{13}C$ signatures in food pathways based on the dominant primary producers were easily detected. Some organisms with known restricted diets, that were closely associated with particular plants in the system, were selected as controls to follow trophic fractionation of $\delta^{13}C$. These included *Uca vocator* from the intertidal forest floor (a mangrove detritus feeder), *Haminoea antillarum* from the middle of the lagoon (an algae grazer), and *Balanus eburneus* and *Isognomon alatus* (filter feeders). Based on results of Fry et al. (1984), we assumed that ^{13}C enriched the isotope ratio by about 1‰ from one trophic level to the next.

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

RESULTS

The Shrimp Community

The shrimp community composition during the study period was similar at the three sampling sites, except that *Penaeus schmitti* were not collected at station 3 (Table 1). *Penaeus notialis* dominated the shrimp assemblage in the lagoon (50.4%), followed by *P. subtilis* (41.1%), and *P. brasiliensis* (8.1%). Only five individuals of *P. schmitti* (0.3%) were collected in 12 months of sampling. Catch per unit effort over time was highly variable for each of the three primary species, with no distinct seasonality (Fig. 1). *Penaeus subtilis*, however, showed a general increase in abundance over the sampling period. *Penaeus brasiliensis* populations remained relatively low and stable throughout the year examined. Population and community structure of the penaeids in Laguna Joyuda has been examined in detail elsewhere (Stoner 1988) and the important point to be made here is that the three most abundant *Penaeus* spp. in Laguna Joyuda are sympatric in both time and space.

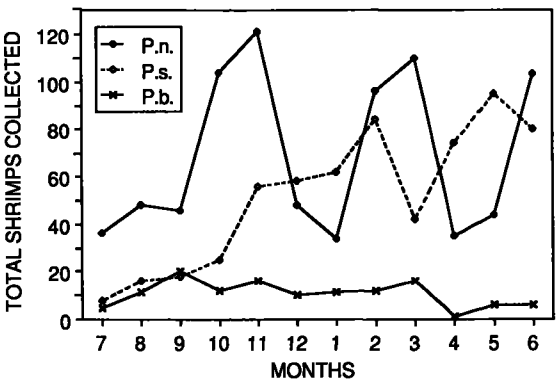

FIGURE 1.—Abundance of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, during the study period. The unit of effort for each sampling date is 18 trawl samples, pooled over all three stations. P.n. = *Penaeus notialis*; P.s. = *P. subtilis*; P.b. = *P. brasiliensis*.

Shrimp Diets

Over 1,300 *Penaeus* guts were examined for the present study. The proventriculi of most individuals contained freshly consumed food items; 89% of all

P. notialis, 87% of all *P. subtilis*, and 78% of all *P. brasiliensis* contained food. At least 50% of all animals in any one size class contained food on a given sampling date, but no seasonal or ontogenetic pattern in empty guts was evident.

The primary dietary components of all three penaeids were amphipods, polychaetes, harpacticoid copepods, and detritus (Fig. 2). For all species increase in shrimp size was correlated with decrease in the relative importance of harpacticoid copepods in the guts. Other small taxa such as nematodes and foraminifera also decreased with shrimp size. Detrital components of the diets remained relatively constant at approximately 20 to 25% of the gut contents. Abundance of polychaetes and amphipods changed relatively little with size in *P. notialis* and *P. subtilis*, except that amphipods increased in importance with size in *P. subtilis* and large quantities of amphipods were taken by the largest size class. Cluster analyses for the diets of individual species revealed little ontogenetic variation for these two species, except with the distinct separation of the largest *P. subtilis* (Fig. 2). For both *P. notialis* and *P. subtilis*, all size classes between 7 and 22 mm CL were clustered within similarity indices of 0.78. Although only three size classes were represented for *P. brasiliensis*, ontogenetic variation in *P. brasiliensis* was greater than in the other two species (Fig. 2). Polychaete consumption decreased from 47% of the diet in the 7 to 10 mm class to 22% in the 15 to 18 mm class, while amphipod consumption increased from 0 to 61%. Detritus consumption also decreased with size in *P. brasiliensis*, contributing to the low similarity indices among the size classes.

Four major clusters of shrimp feeding types were

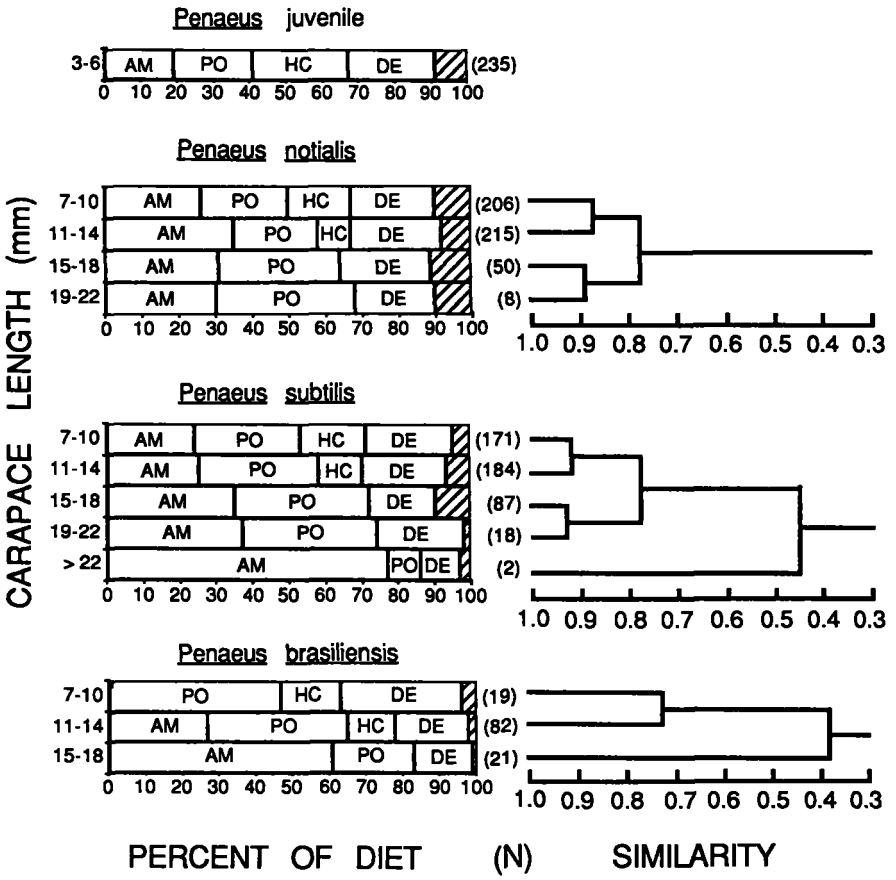

FIGURE 2.—Diets of the three dominant *Penaeus* species in Laguna Joyuda, Puerto Rico, shown as a function of shrimp size. Food categories are identified in Table 2. The similarity index used in the cluster diagrams is Czekanowski's coefficient.

revealed when the full matrix of similarity indices, including all species and size classes, was incorporated into a cluster analysis (Fig. 3). The greater ontogenetic variation in diets of *P. brasiliensis* resulted in the three size classes for the species falling into three distinct clusters, while all four size classes of *P. notialis* were included under two clusters. The largest *P. subtilis* were clustered with the largest *P. brasiliensis*. Except for *P. brasiliensis*, all shrimps between 7 and 14 mm CL were found in one trophic group and all between 15 and 22 mm CL were found in a second group.

Species or generic level identification of prey organisms indicated no species-specific differences among the diets of the three shrimp species. For all three species, all amphipods identifiable to species were *Grandidierella bonnieroides* and all identifiable polychaetes were nereids (probably *Nereis occidentalis* and *Steninonereis martini*). In *P. subtilis* and *P. brasiliensis*, all harpacticoid copepods were *Euterpina* spp. In *P. notialis*, 86% were *Euterpina* spp. and 14% were *Microsetella* sp. The calanoid copepods were a mixture of *Acartia tonsa* and *Pseudodiaptomus* spp.

Animals classified in groups 2 and 3 of the multispecies cluster (Fig. 3) contained sufficient numbers of individuals to make seasonal analyses of diets (Figs. 4, 5). Although harpacticoid copepods were taken in lower amounts by group 3 shrimps, by and large both groups showed similar seasonal trends in diet. Amphipods were taken in large numbers from July to October 1985 and from March through June 1986. Polychaetes and harpacticoid copepods were consumed most abundantly in November through March. Consumption of detritus was relatively constant in both groups, with slightly higher detrital intakes in group 2 individuals during November and December 1984.

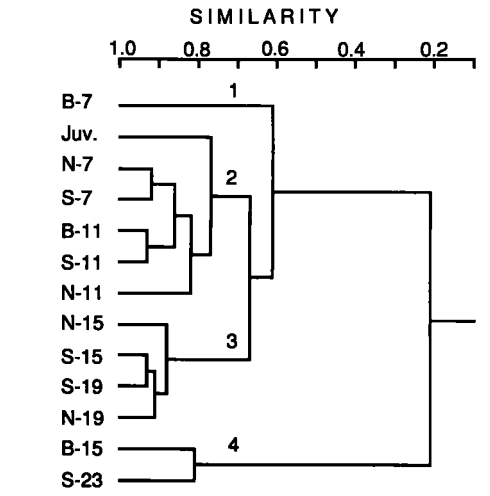

FIGURE 3.—Cluster diagram for the diets of shrimps incorporating all species and size classes. The cluster strategy is the same as that in Figure 2. Food categories are identified in Table 2.

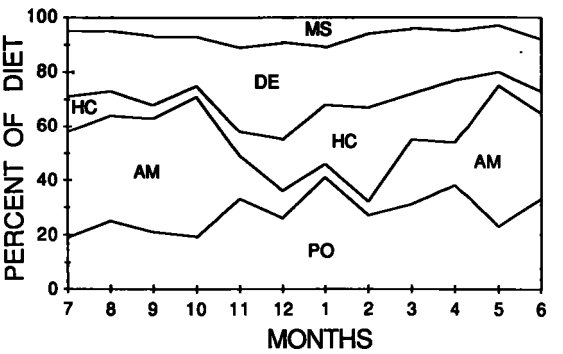

FIGURE 4.—Diets of shrimp trophic group 2 by sampling date.

Carbon Isotopes

The $\delta^{13}C$ values for three different samples of tissues from *Penaeus* spp. ranged from −15.0 to −18.1‰ (Table 3). These values were much higher than the plankton fraction <35 μ (comprised primarily of dinoflagellates; −26.8 to −27.2‰) or the primary copepod species in the lagoon, *Acartia tonsa* (−24.0 to −25.9‰). The $\delta^{13}C$ values for the shrimps are also much higher than the values for either mangrove leaves (green or dead), or detritus particles from the sediment, mostly of mangrove origin. The only primary producers with $\delta^{13}C$ values within the range of *Penaeus* spp. were the seagrass *Thalassia testudinum* (−16.1‰) and the

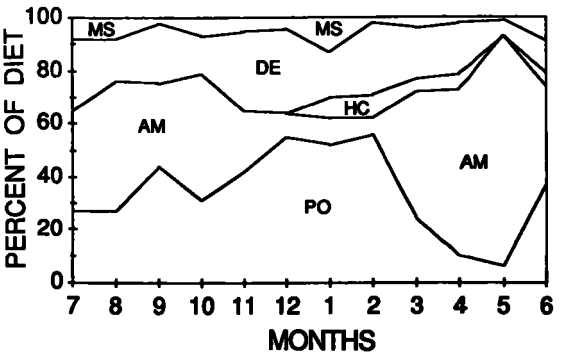

FIGURE 5.—Diets of shrimp trophic group 3 by sampling date.

algal mat comprised primarily of the filamentous blue-green alga *Spirulina* sp. Because there are only small patches of *T. testudinum* in Laguna Joyuda and the blue-green algae dominated the lagoon floor, the data suggest that the main source of carbon for penaeid shrimps in Laguna Joyuda is benthic blue-green algae. Blue-green algae also appear to be the primary source of carbon for other decapod crustaceans in the lagoon including *Callinectes* spp. and hermit crabs (Paguridae) (Table 3).

The carbon isotope data, suggesting algal sources of carbon for *Penaeus* spp., are consistent with the results of dietary analyses. The primary prey of penaeids were the amphipod *Grandidierella bonnieroides* and capitellid polychaetes. The $\delta^{13}C$ value for *G. bonnieroides* was within the range for *Penaeus* spp., −17.7‰. Similarly, when the bodies of capitellids were analyzed after removal of the guts, the $\delta^{13}C$ value of −18.8‰ also agrees with shrimps after adjusting for trophic fractionation of 1‰ less (Fry et al. 1984). Other organisms with $\delta^{13}C$ values similar to that of blue-green algae were the bubble snail *Haminoea antillarum* and the bivalve *Macoma brevifrons*. The carbon isotope ratios of these benthic feeders were more negative than *Spirulina* (−14.1‰), implying modification of $\delta^{13}C$ values from other sources; however, the major input appears to be from blue-green alga.

By contrast, organisms associated with the mangrove forest, *Uca vocator* (−23.0‰) and *Aratus pisonii* (−23.3‰), closely resembled carbon isotope ratios of detritus (−22.9 to −25.0‰). Moreover, the <35 μ plankton fraction (−26.8 to −27.0‰) and associated grazers, *Acartia* (−24.0 to −25.9‰), *Balanus* (−24.0‰), and *Isognomon* (−24.4‰), were not separable from the mangrove group. These data indicate that mangrove carbon is likely being incorporated into plankton-based food

TABLE 3.—Carbon isotope ratios in organisms associated with the penaeid shrimp food web in Laguna Joyuda, Puerto Rico.

Organisms	Tissue or composition	Number of pooled indiv.	Date of collection	$\delta^{13}C$
Plankton				
<35μ fraction		—	9/29/83	−26.8 to −27.2
Acartia tonsa	whole bodies	500	1/21/81	−25.9
Acartia tonsa	whole bodies	500	9/8/83	−25.2
Acartia tonsa	whole bodies	500	9/27/83	−24.0
Macroalgae				
Spirulina sp.	entire filaments	—	2/14/83	−14.2
Caulerpa sertularoides	entire alga	—	9/29/83	−20.2
Seagrass				
Thalassia testudinum	green leaves	—	9/29/83	−16.1
Mangroves				
Avicennia germinans	roots	—	2/14/84	−24.0
Rhizophora mangle	green leaves	—	9/24/81	−29.2
Rhizophora mangle	dead leaves	—	2/14/84	−27.3
Detritus				
Particules from the sediment		—	9/24/81	−22.9 to −25.0
Polychaetes				
Capitellidae	body without gut	13	9/24/81	−18.8
Capitellidae	whole bodies	10	2/14/81	−23.1
Capitellidae	whole bodies	10	9/30/81	−22.0
Capitellidae	whole bodies	10	2/14/84	−22.9
Nereidae	whole bodies	2	2/14/84	−21.6
Mollusca				
Haminoea antillarum	whole bodies	1	9/24/81	−15.8
Isognomon alatus	whole bodies	6	9/24/81	−24.4
Macoma brevifrons	whole bodies	6	9/24/81	−18.8
Crustacea				
Aratus pisonii	leg muscle	10	9/30/81	−23.3
Balanus eburneus	whole bodies	20	9/24/81	−24.0
Callinectes danae	claw muscle	2	2/14/84	−15.4
Callinectes sapidus	claw muscle	1	2/14/84	−16.4
Grandidierella bonnieroides	whole bodies	52	2/14/84	−17.7
Pagurus sp.	leg muscle	3	2/14/84	−16.2
Penaeus notialis	tail muscle	12	9/31/81	−18.1
Penaeus notialis	tail muscle	10	2/14/84	−15.4
Penaeus subtilis	tail muscle	10	2/14/84	−15.0
Petrolisthes sp.	whole bodies	12	9/24/81	−23.5
Uca vocator	leg muscle	10	9/30/81	−23.0

chains in the lagoon. This can be supported using *Acartia* as a link, since the copepod is known to feed on detritus particles and because the growth of *Acartia* is improved with detritus is included in the diet (Roman 1984). Suspended detritus particles from mangroves were a component of our <35 μ plankton fraction, suggesting availability to planktonic consumers.

DISCUSSION

Early studies of penaeid diets led to the general conclusion that the shrimps were largely detritivorous with incidental amounts of animal or plant material in the guts (Williams 1955; Darnell 1958; Odum and Heald 1972). Dall (1968) concluded that several Australian penaeids were not predators, but consumers of small-sized and disabled animals. Although penaeid shrimps are known to sort sediments for organic particles with their delicate pereiopods (Dall 1968; Lindner and Cook 1970) it is now apparent that penaeid shrimps are capable of taking prey organisms such as large polychaetes, as well as the more difficult prey such as gastropods and bivalves, caridean shrimps, crabs, echinoderms, and even fishes (Moriarty 1977; Marte 1980; Leber 1983). Lindner and Cook (1970) reported that *Penaeus setiferus* is cannibalistic at times. The relatively constant low amount of detrital particles in the guts of shrimp from Laguna Joyuda suggests that the less readily digestible detritus is taken incidentally with animal prey or as a response to low prey abundance. In addition, Gleason and Zimmerman (1984) showed that nematodes, oligochaetes, polychaetes, and copepods were stripped from detritus by *P. aztecus* during feeding. Reports of shrimp filled with unrecognizable debris assumed to be detritus may be a consequence of actual detritus consumption or incomplete development of methods sufficient to make animal remains identifiable.

Despite considerable attention given to feeding in the commercially significant penaeids, relatively few investigators have examined ontogenetic variation in diets. In this study, even within juvenile size classes, there were clear patterns of dietary change with shrimp size. All three of the subject species abandoned smaller prey organisms such as foraminifera, nematodes, and harpacticoid copepods in favor of amphipods, polychaetes, and shrimp as the predators became larger. Similar findings were reported by Leber (1983) for *P. duorarum*. These ontogenetic shifts in prey are undoubtedly related to increasing size of the chelae and mouth parts and must be considered in any ecological interpretation of trophic position; Moriarty (1977) suggested that the great opportunism of penaeid shrimps precluded their being placed in one trophic group throughout their life cycle.

On the other hand, with the exception of accelerated ontogenetic shifts in the diets of *P. brasiliensis*, interspecific variation in feeding in Laguna Joyuda were relatively minor. Despite high abundance and great temporal and spatial overlap in the *Penaeus* spp. of the lagoon (Stoner 1988), coupled with very low biomass values for macrofauna (<2 g dry wt/m^2), there is no evidence for resource partitioning among the grooved shrimps.

Seasonal diets in *Penaeus* spp. were coincident with seasonal trends in the abundance of major prey organisms. In the lagoon, the one important amphipod species, *Grandidierella bonnieroides*, demonstrated maxima between July and September and again from May to June; this corresponded with maximum amphipod consumption between July and October and March through June in the same year as benthic studies. Polychaete consumption was highest between November and March (particularly in the group 3 shrimps), corresponding with the October to April peak in capitellid abundance in the lagoon. Consequently, the oscillation in polychaete and amphipod feeding appears to be related to the availability of foods.

The hypothesis that mangrove estuaries are fueled primarily by carbon from mangrove detritus has become established from the pioneering work on mangrove-associated food webs conducted in the North River estuary of south Florida (Odum and Heald 1972, 1975). Mangrove litter inputs to Laguna Joyuda are high (Levine 1981), the sediments are rich in organic content, and detritus comprised a portion of the gut contents of juvenile shrimp. It is unlikely, however, that a large amount of carbon derived from detritus or detritus-associated microbes contributes in a large way to the tissues of the shrimp in the lagoon. In fact, the only organisms which had carbon isotope ratios similar to that of detritus were those normally found in direct association with the trees such as fiddler and mangrove crabs. The $\delta^{13}C$ values for shrimp in Laguna Joyuda were, in fact, very similar to values for penaeids from the open waters of the Gulf of Mexico (Fry and Parker 1979).

Benthic algal primary production in Laguna Joyuda is probably highly significant because carbon isotope ratios in the algae and shrimp were similar. Gleason (1986) also found that juvenile *P. aztecus* penaeids in a Galveston Bay salt marsh derived their carbon from blue-green algae, green

algae, and epiphytes of salt marsh grasses, not from *Spartina* detritus. Algal foods also proved to be the primary source of carbon for penaeids in Georgia marshes (Hughes and Sherr 1983) and in *P. duorarum* inhabiting seagrass beds in the Gulf of Mexico (Leber 1983) where food webs have long been considered detritus based. The significance of algal production in mangrove areas has been pointed out by Rodelli et al. (1984). They concluded that both mangrove and algal carbon were utilized by most of animals in a Malaysian swamp, but virtually no animals collected at distances >2 km from the swamp contained mangrove-derived carbon. To this date, there is little evidence to suggest that natant species such as fishes and decapod Crustacea can use detritus as a primary food source even if microbially enriched (Boesch and Turner 1984).

Localities where mangroves grow often support a variety of other primary producers, and variation in the relative significance of detrital and algal carbon sources may be associated with tidal amplitude and flushing. Laguna Joyuda, with microtidal influences, appears to be fueled by algal carbon whereas shrimp-producing mangrove areas in Ecuador have meso- and macrotidal regimes and no apparent algal growth (Zimmerman, pers. observ.). That mangroves provide critical substratum and protective cover for a large number of organisms is undisputed; however, the assumed significance of mangrove-derived detritus should be examined further.

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THE EFFECT OF THE ECTOPARASITIC PYRAMIDELLID SNAIL, *BOONEA IMPRESSA*, ON THE GROWTH AND HEALTH OF OYSTERS, *CRASSOSTREA VIRGINICA*, UNDER FIELD CONDITIONS

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ABSTRACT

Boonea (= *Odostomia*) *impressa* are contagiously distributed on oyster reefs so that some oysters are parasitized more than others. The parasite's mobility and the ability of oysters to recover from snail parasitism may be important in assessing the impact of parasitism on oyster populations. During a 4-week exposure period in the field, *B. impressa* reduced American oyster, *Crassostrea virginica*, growth rate and increased the intensity of infection by the protozoan, *Perkinsus* (= *Dermocystidium*) *marinus*, but produced few changes in the oyster's biochemical composition because, although net productivity was reduced, the oysters retained a net positive energy balance (assimilation > respiration). During a 4-week recovery period, growth rate returned to normal (control) levels, but infection by *P. marinus* continued to intensify in previously parasitized oysters kept *B. impressa*-free. Most changes in biochemical composition during recovery, including increased lipid and glycogen contents, could be attributed to the continuing increase in infection intensity of *P. marinus*. Consequently, the temporal stability and size of snail patches, particularly as they regulate infection by *P. marinus*, may be the most important factors influencing the impact of *B. impressa* on oyster reefs.

Parasitism can be an important factor affecting the population dynamics (Wickham 1986; Brown and Brown 1986; Kabat 1986) and health (Brockelman 1978; Mohamed and Ishak 1981; Ford 1986) of host species. Three parasites are known to be especially important in oysters. *Perkinsus* (= *Dermocystidium*) *marinus*, *Haplosporidium nelsoni* (MSX), and *Boonea* (= *Odostomia*) *impressa* detrimentally affect oyster growth, health, and biochemical composition (Mengebier and Wood 1969; Feng et al. 1970; Soniat and Koenig 1982; White et al. 1984; Ford 1986; Ward and Langdon 1986; White et al. 1988, in press).

The pyramidellid gastropod, *Boonea impressa*, is one of a widely distributed group of parasitic, marine opisthobranchs (Fretter and Graham 1949; Fretter 1951; Allen 1958). *Boonea impressa* removes nutrients directly from its host by piercing the flesh with a hollow stylet and sucking the body fluids using a buccal pump (Fretter and Graham 1949; Fretter 1951; Allen 1958). The most common host of *B. impressa* is *Crassostrea virginica* (Hopkins 1956; Allen 1958; Wells 1959) but, like other odostomians, it is not entirely host specific (Wells 1959; Robertson 1978; Robertson and Mau-Lastovicka 1979). Found abundantly on oyster reefs from Massachusetts to the Gulf of Mexico, *B. impressa* has been reported in numbers as high as 100 per oyster (Hopkins 1956).

Under laboratory conditions, *B. impressa* reduced oyster growth rates as the result of both direct removal of assimilated carbon from the oyster and direct interference with the oyster's ability to feed (White et al. 1984, 1988; Ward and Langdon 1986). Not surprisingly, parasitism by *B. impressa* produced changes in the biochemical composition of oyster tissue. Parasitism by 15 snails, a relatively high field density found in dense snail patches decreased carbohydrate and free amino acid content and increased lipid content of mantle tissue. Reproduction was affected as well (White et al. in press).

Perkinsus marinus is an important cause of mortality of oysters in the Gulf of Mexico (Mackin 1962; Ray 1966a; Hofstetter 1977). Sublethal effects include reduced growth (Menzel and Hopkins 1955; Ray et al. 1953) and changes in biochemical composition (Soniat and Koenig 1982; White et al. in press). *Perkinsus marinus* can be transmitted from one oyster to another through the water (Ray 1954; Mackin 1962; Andrews 1965) or by *B. impressa* feeding (White et al. 1987). The intensity of infection by *P. marinus* is also increased in *B. impressa*-parasitized oysters (White et al. 1987).

Usually stress affects organisms by altering normal metabolic activity. Many organisms may be able

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to return to normal metabolic condition after the stress is removed (Pörtner et al. 1979; Pickering et al. 1982; Kendall et al. 1984). This ability, termed recovery, is an important adaptation to changes in the natural environment. Recovery is not always complete nor does it occur over relatively short time scales in all cases. The time required for recovery varies depending on the parameter being studied, the stress that was applied, and the species involved (Kendall et al. 1984; Haux et al. 1985; Neff et al. 1985). Apparently deleterious effects occurring after exposure, during the so-called recovery period, are well described (e.g. Kendall et al. 1984; Powell et al. 1984). White et al. (1984) showed that *C. virginica* could attain normal growth rates within one week after *B. impressa* were removed. However, growth rates frequently return to normal more rapidly than other metabolic parameters (Kendall et al. 1984). *Boonea impressa* are extremely mobile and are more contagiously distributed than their hosts, so that some oysters are highly parasitized while others remain parasite free (Powell et al. 1987). Individual *B. impressa* change hosts often but typically move between existing aggregates (Wilson et al. in press). Therefore, refugia from parasitism may exist and recovery may be important in assessing the overall impact of *B. impressa* on oysters.

Stress, produced by laboratory conditions, frequently accompanies laboratory experimentation (e.g., Koenig et al. 1981; Powell et al. 1984; Kukal and Kevan 1987). The effect of *B. impressa* on *C. virginica* has been assessed primarily through laboratory experimentation. Consequently, we examined the effect of *B. impressa* on *C. virginica* under field conditions and assessed the ability of oysters to recover normal growth rates and biochemical composition once snail parasitism ceased.

MATERIALS AND METHODS

Field Study

Oysters and snails used in this study were collected at Goose Island State Recreation Area near Rockport, TX. The oysters were weighed on a Mettler balance using the underwater method of Andrews (1961). Fifteen oysters (precontrols) were sacrificed to define the biochemical composition of the oysters and *Perkinsus marinus* levels that existed naturally at the collection site. The rest of the oysters were placed in semi-enclosed plexiglass domes (see figure 2 in Kendall et al. 1984 for description) in a tidal creek near the Aransas Pass Lighthouse on Lydia Ann Channel, near Port Aransas, TX. The domes allowed water to circulate over the oysters, while excluding such large predators as oyster drills and crabs. *Boonea impressa*, however, could readily move into or out of the domes.

Two of the four domes (20 oysters per dome) contained oysters exposed to *B. impressa* at a concentration of 10 snails per oyster, a level of parasitism commonly observed on reefs in the collection area (White et al. 1984). The domes were positioned so that the probability of snails moving from the exposure domes with parasitized oysters to the control domes was minimized (Fig. 1). Snails on each experimental oyster were counted twice weekly for 4 weeks. No *B. impressa* were ever found on control oysters. *Boonea impressa* did emigrate from the exposure domes, however, so snails were added as needed to maintain the 10:1, snail:oyster ratio. Control oysters were handled the same as experimentals each week in an effort to minimize differential effects caused by handling stress (see Pickering et al. 1982; Andrews and Hewatt [1957] were unable to find any effect of handling on *P. marinus* infection in oysters).

At the end of 4 weeks, the oysters were reweighed and half from each dome were sacrificed. The remaining oysters were replaced in the field for a 4-wk recovery period without *B. impressa*. All *B. impressa* were removed from the previously parasitized oysters by hand prior to replacement. The domes were visited twice weekly and each oyster handled as before. No *B. impressa* were found on the oysters during the recovery period.

Laboratory Analysis

Perkinsus marinus infection was measured in each oyster by incubating a small piece of mantle tissue in thioglycollate medium by the method of Ray (1966b). Intensity of infection was based on a semi-quantitative 0 to 5 rating assigned during microscopic inspection of the tissue after treatment with Lugol's solution (Mackin 1962). Small pieces of gonadal tissue were preserved in Bouin's fixative, sectioned and stained in 0.5% toluidine blue (Preece 1972) for gonadal analysis. Mantle cavity volume was determined by filling the shells with silicon caulking. Oyster growth, as expressed by shell deposition, was measured using the underwater weighing method. Condition index was derived by dividing the total lyophilized dry weight by the mantle cavity volume (Lawrence and Scott 1982).

The mantle and adductor muscle from each oyster

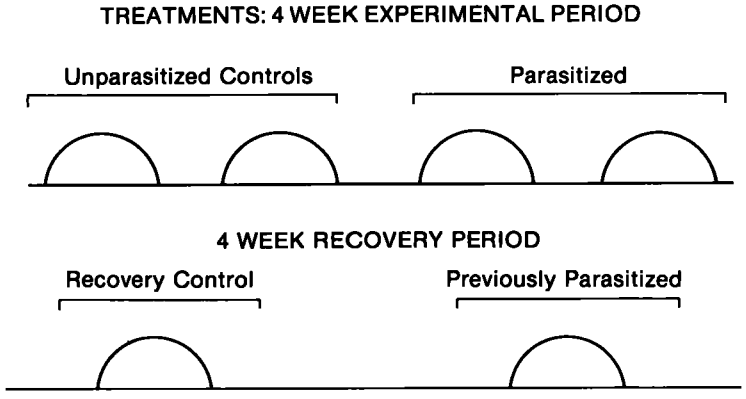

FIGURE 1.—Position of plexiglass domes during 4-wk experimental period and during 4-wk recovery period.

were frozen immediately on dry ice and kept at −40°C until lyophilized. Prior to biochemical analysis, lyophilized tissues were weighed and homogenized on ice. Total lipids were isolated from a portion of the homogenate using the water:methanol: chloroform method of Folch et al. (1957) with a modified ratio of 0.8:2.1. This isolation produced a two phase system and an insoluble pellet after centrifugation in the cold. The pellet was used for protein and glycogen assays. The water phase was used for amino acid analysis. The organic phase was divided and dried under N_2 gas at 40°C. One half was used to determine lipid phosphate concentration by the spectrophotometric method of White et al. (1979). The other half was dissolved in chloroform to which nonadecanoic acid was added as an internal standard. The redissolved lipids were fractionated on a silicic acid (Unisil,[3] 100–200 mesh) column. Neutral lipids were recovered by eluting with 10 times the column volume of chloroform. The chloroform was removed under N_2 at 40°C (Gehron and White 1982). The resulting chloroform fraction, containing fatty acid methyl esters, was analyzed by gas chromatography using a capillary, nonpolar, methyl silicone high performance column and flame ionization detector.

The amino acids were analyzed on a Dionex 3000 amino acid analyzer. Because residual chloroform interfered with the analysis, a second extraction was performed on the sample in the cold using a chloroform:water ratio of 1:3; *α*-amino-*n*-butyric acid (2.5 μmole · mL^{-1} sample) was used as an internal standard. The amino acids accounting for the bulk of the free amino acid (FAA) pool, taurine, hypotaurine, aspartic acid, serine, threonine, glutamine, glutamate, glycine, and alanine, were separated using a lithium citrate buffer and measured using *o*-phthalaldehyde as the detecting compound.

Total soluble protein was estimated by Peterson's (1977) modification of the Lowry method. Protein was precipitated using a final concentration of 10% trichloroacetic acid in the cold. After centrifugation at 4°C the resultant pellets were resuspended in 50:50, 10% SDS:0.8N NaOH for 30 minutes. Replicate samples were centrifuged and analyzed spectrophotometrically for protein concentration. Bovine serum albumin (Sigma) was used as the standard.

Glycogen was degraded to glucose enzymatically with amyloglucosidase (Carr and Neff 1984). After preincubation with amyloglucosidase, glucose was measured using the glucose oxidase-peroxidase procedure (Sigma glucose kit) (Roehrig and Allred 1974). Rat liver glycogen (Sigma) was used as a standard.

Statistical Analysis

To assess the effect of *Boonea impressa* on the oysters during the 4-wk exposure period, the level of snail parasitism for each oyster had to be determined. Because the number of snails on each oyster was counted only every third day, the total number of snails that parasitized each oyster was estimated by assuming that the same number of snails were present on days between counts as found on the previous visit. The total number of snail-days per oyster, the sum of the number of snails present on each day during the 4-wk exposure, will be referred to as the snail scale. For example, during the first week of the exposure period, one oyster had 15

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

snails on Monday, 10 on Wednesday, and 4 on Saturday; therefore Tuesday was assigned 15 snails, Thursday and Friday 10 snails, and the total for the week was 64 snail-days.

Except where noted in the text, results were analyzed by multiple analysis of covariance (MANCOVA) using ranked data followed by Duncan's multiple range tests ($\alpha = 0.05$) to locate significant differences within the MANCOVA. Mantle cavity volume was used as the covariate for comparing levels of *P. marinus* infection intensity, dry weight, and shell weight gain between treatment groups (e.g., parasitized and control oysters). Similar tests comparing biochemical parameters between treatment groups included the intensity of *P. marinus* infection and tissue dry weight as covariates. When the requirement of parallelism was not met, the MANCOVA was modified as described by Smith and Coull (1987). *Perkinsus marinus* infection intensity was used as both a dependent and independent variable because, although *B. impressa* can influence the intensity of *P. marinus* infection (White et al. 1987), *P. marinus* itself can affect the biochemical composition of oysters (Soniat and Koenig 1982; White et al. in press). Only parasitized oysters (or those recovering from parasitism) were used in analyses of the effect of snail scale (intensity of parasitism).

The FAA pool was analyzed three ways: 1) the entire pool, 2) the pool minus taurine and hypotaurine because these are the only amino acids not found in protein, and 3) after exclusion of the major components (taurine, hypotaurine, glycine, and alanine) so that changes in the lesser constituents of the pool could be examined.

All analyses for the 4-wk exposure period used MANCOVA analyses with nested variables, which took into account which of the 4 domes the oysters were in during the exposure period. Overall, significant differences in biochemical composition (i.e., amino acid content, glycogen, protein, etc.) between the 2 nonparasitized domes or between the 2 snail parasitized domes did not occur more frequently than expected by chance (Binomial Test, $\alpha = 0.05$). Therefore, the two equivalently treated domes of each treatment group (Fig. 1) were lumped together for comparison with precontrol and recovery oysters. Nevertheless, the experimental design represents a case of pseudoreplication; hence the caveats of Hurlbert (1984) should be considered when reviewing the statistical analysis.

RESULTS

Growth, *Perkinsus marinus* Intensity, and Reproduction

Boonea impressa affected oyster growth rate, the intensity of infection by *P. marinus*, and reproductive state. The mean initial shell weights of the precontrol, control, and parasitized groups were not significantly different from each other. By the end of the 4-wk exposure period, both parasitized and unparasitized oysters had gained weight, but oysters parasitized by *B. impressa* gained significantly less weight than unparasitized oysters (Table 1). Oysters with more snails typically gained less weight than oysters with fewer snails. The relationship between the intensity of *B. impressa* parasitism (snail scale) and weight gain among parasitized oysters was significant (Spearman's rank, $P = 0.03$; weight gain normalized to initial weight, $P = 0.001$, Fig. 2).

Mantle cavity volume did not vary among any of the treatment or recovery groups. Condition index was not significantly different between treatment groups or between recovery groups. Condition index was significantly higher in the two recovery

TABLE 1.—Mean and standard deviations for initial shell weight (g) and average shell weight gain per oyster during the 4-wk exposure period and 4-wk recovery period. Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$). A test was restricted to a single column. Groups having the same letter within a column are not significantly different.

	Initial weight		Weight gained during 4-wk exposure		Weight gained during 4-wk recovery	
Group	Mean ± SD	Sig.	Mean ± SD	Sig.	Mean ± SD	Sig.
Precontrol (n = 15)	22.82 ± 12.16	A				
Treatment						
Control (n = 40)	17.16 ± 8.48	A	3.49 ± 1.21	A		
Parasitized (n = 40)	16.84 ± 7.47	A	2.54 ± 1.31	B		
Recovery						
Control (n = 6)					2.16 ± 0.73	B
Previously parasitized (n = 15)					2.89 ± 1.05	A

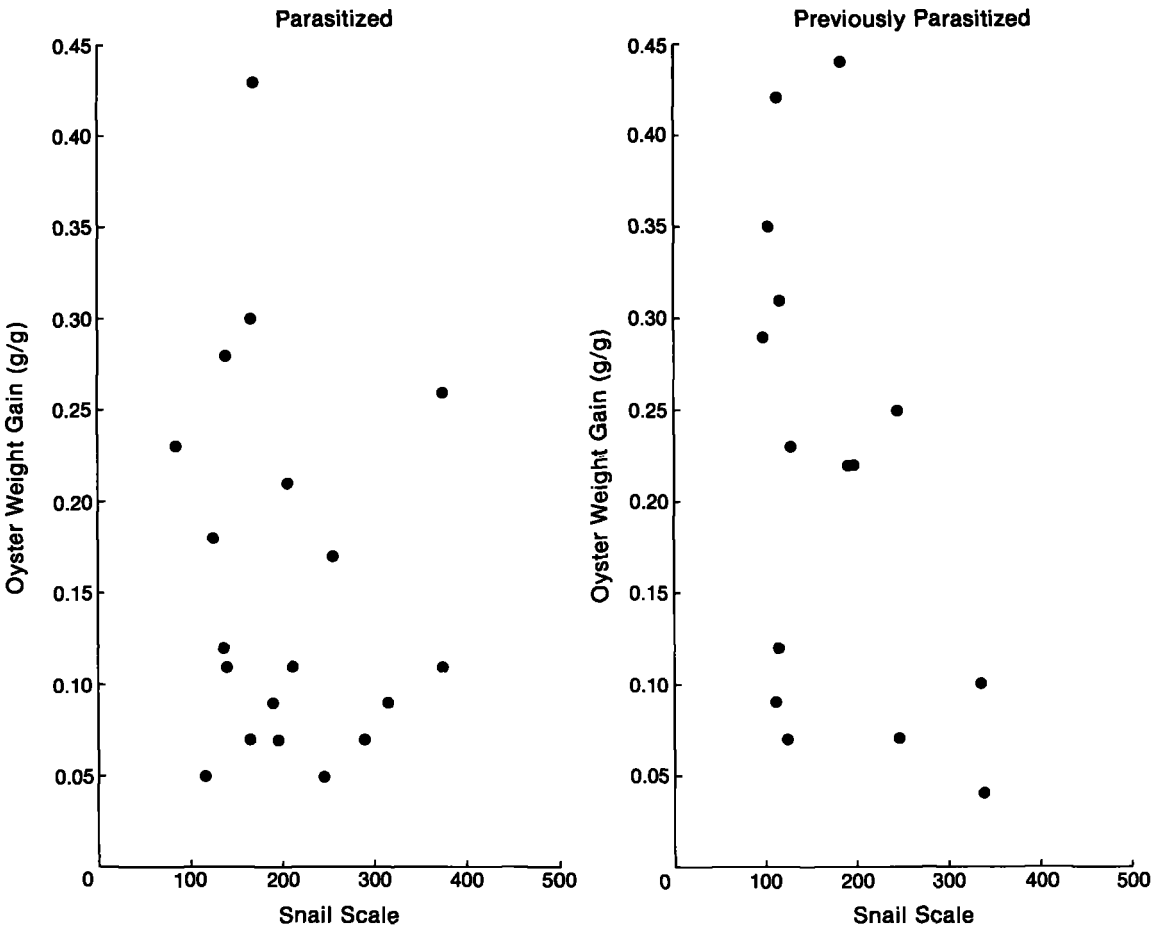

FIGURE 2.—Left: Weight gain (g) per g initial weight of individual snail-parasitized oysters after the 4-wk experimental period as a function of the level of *Boonea impressa* parasitism, or snail scale. Right: Weight gain (g) per g initial weight of individual oysters after the 4-wk recovery period as a function of the level of *B. impressa* (snail scale) during the 4-wk treatment period.

groups than in the treatment and precontrol groups (Table 2).

During the recovery period, when all oysters were parasite-free, the previously parasitized oysters (those with snails during the treatment period) gained significantly more weight than the recovery controls (Table 1). Oysters which were previously parasitized by fewer *B. impressa* during the treatment period gained more weight during the recovery period than those that were previously parasitized by more snails (Spearman's Rank correlation, $P = 0.07$, Fig. 2), but the relationship was considerably weaker than during the treatment period.

The intensity of infection by *P. marinus* increased throughout the experiment in parasitized oysters so that, after recovery, previously parasitized oysters had higher prevalences and intensities of infection than they did after 4 weeks of parasitism; these values in turn were higher than the precontrol values at the experiment's inception (Table 3). Exactly the opposite trend occurred in control oysters. Recovery controls had the lowest values of prevalence and intensity. Consequently, after the recovery period, previously parasitized oysters had significantly higher intensities of infection than recovery controls. The proportion of infected individuals (33% of the controls, 93% of the previously parasitized oysters) was significantly higher as well (χ^2, $P < 0.05$). Within the parasitized oysters, the intensity of parasitism (snail scale) did not correlate with the increase in intensity of *P. marinus* infection during either the treatment or recovery period (Fig. 3, Spearman's Rank, $P > 0.05$; the interaction

TABLE 2.—Means and standard deviations for volume (mL), condition index ($g \cdot mL^{-1}$) and dry weight (g). Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$). A test was restricted to a single column. Groups having the same letter within a column are not significantly different. *n*, see Table 1.

Group	Volume Mean ± SD	Sig.	Condition Index Mean ± SD	Sig.	Dry weight Mean ± SD	Sig.
Precontrol	10.4 ± 4.1	A	3.4 ± 0.8	C	0.35 ± 0.14	AB
Treatment						
Control	11.2 ± 3.6	A	5.4 ± 1.0	B	0.34 ± 0.11	AB
Parasitized	9.2 ± 1.7	A	5.5 ± 1.0	B	0.28 ± 0.12	B
Recovery						
Control	9.5 ± 4.6	A	7.1 ± 1.5	A	0.32 ± 0.14	B
Previously parasitized	10.8 ± 3.8	A	7.7 ± 1.5	A	0.51 ± 0.24	A

TABLE 3.—Mean and standard deviations for *Perkinsus marinus* infection intensity among groups. Significance levels from Duncan's multiple range test ($\alpha = 0.05$) apply to the infection intensity data. Groups with the same letter are not significantly different. Percent incidence is the number of oysters infected divided by the number of oysters in the sample. Infection intensity was calculated using the 5-point scale of Mackin (1962). *n*, see Table 1.

Group	*Perkinsus marinus* Infection Intensity Mean ± SD	Significance	Prevalence
Precontrol	1.47 ± 1.45	AB	66.6
Treatment			
Control	1.10 ± 1.06	AB	65.0
Parasitized	1.63 ± 1.32	AB	79.0
Recovery			
Control	0.83 ± 1.60	B	33.3
Previously parasitized	2.21 ± 1.38	A	92.9

TABLE 4.—Results of histological examination of gonadal samples for each group. Significance levels (sig.) from Duncan's multiple range test ($\alpha = 0.05$) are for differences in the number of eggs present per female in a histological section. Percent of females spawning is the number of females with eggs observed in the gonoducts divided by the number of females in the sample.

Group	Sex Female	Male	Eggs present Mean ± SD	Sig.	Percent of females spawning
Precontrol	7	7	31.1 ± 4.4	A	86.0
Treatment					
Control	6	4	36.6 ± 11.0	A	100.0
Parasitized	4	6	21.6 ± 3.9	B	100.0
Recovery					
Control	5	1	37.6 ± 6.0	A	80.0
Previously parasitized	11	4	42.9 ± 9.8	A	81.0

term in the MANCOVA was also nonsignificant).

The number of eggs per microscopic field estimated from histological sections, was significantly lower in parasitized oysters after the 4-wk treatment period (Table 4). No differences between controls and previously parasitized oysters were present after the 4-wk recovery period. The proportion of oysters ready to spawn (female oysters which had eggs visible in the gonoducts) was not significantly different in parasitized and unparasitized oysters during treatment or recovery (χ^2, $\alpha = 0.05$).

Biochemical Composition

Mean levels of the various biochemical components measured in adductor muscle and mantle tissue are given in Tables 5 and 6. A comparison of precontrol, treatment control, and recovery control oysters documents the changes in biochemical composition produced by handling stress and natural environmental changes that occurred during the experiment. Glycogen increased significantly in the mantle tissue during the 4-wk treatment period, then decreased during the recovery period (Table 7). Glycogen in the adductor muscle also decreased during the recovery period (Table 7). Hypotaurine increased in both tissues during the treatment period (Table 8). Most other FAA and the total pool dropped in concentration in the mantle tissue in the first 4 weeks, but then stabilized. In contrast, in the adductor muscle, significant increases in glycine and hypotaurine during the treatment period were offset by a significant decrease in alanine, so the total pool changed little. Again, the FAA pool stabilized during the first 4 weeks. Hence, there was little difference in treatment and recovery controls in any measured biochemical component.

Snail parasitized and control oysters did not differ significantly in the concentration of any of the biochemical components in either the mantle or adductor muscle (Tables 7, 8). Only one biochemical parameter differed between the recovery control

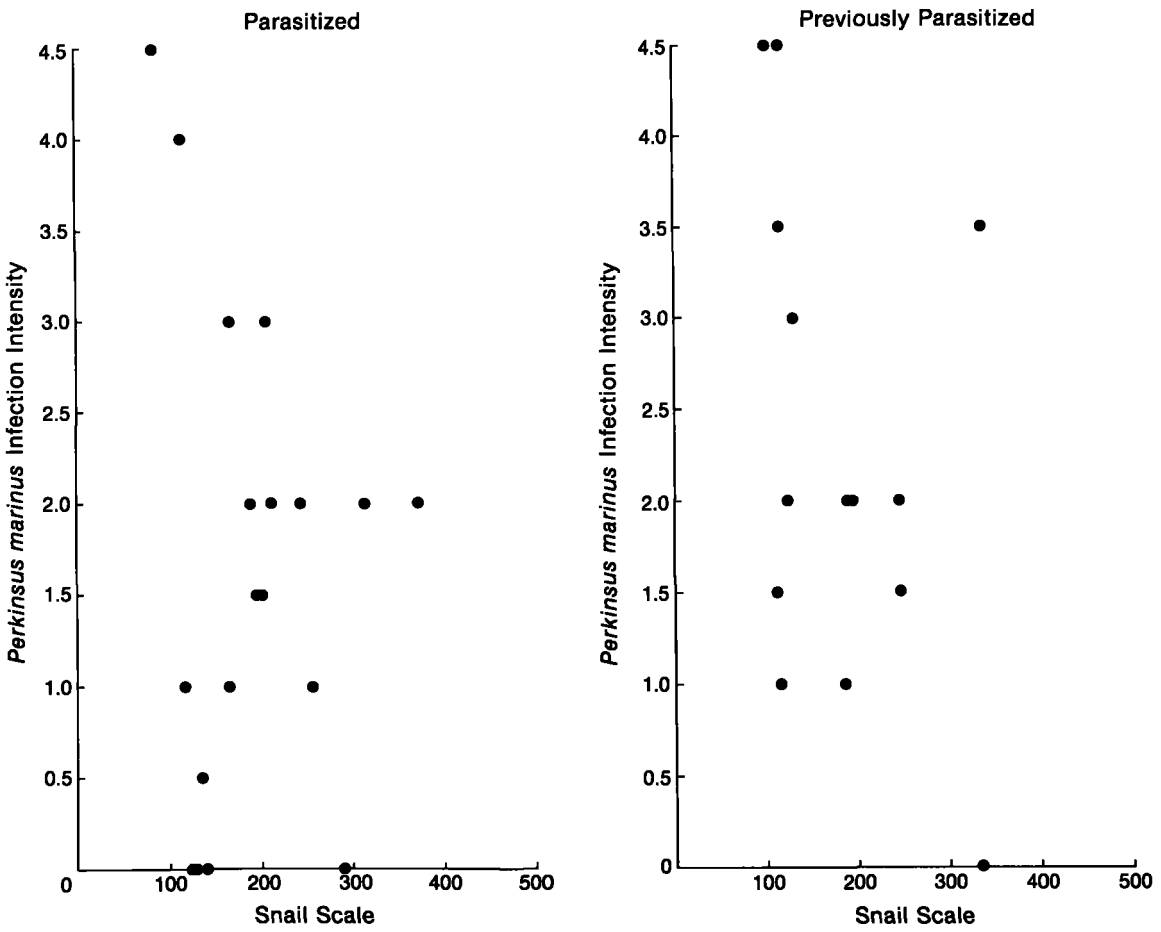

FIGURE 3.—Left: Intensity of *Perkinsus marinus* infection in snail-parasitized oysters as a function of the level of snail parasitism after the 4-wk treatment period. Right: Intensity of *P. marinus* infection in previously snail-parasitized oysters as a function of the level of snail parasitism after the 4-wk recovery period.

and previously parasitized oysters. Recovery controls had significantly less glycogen in the mantle tissue (Table 7). No biochemical component was significantly correlated with the intensity of snail parasitism (snail scale) in parasitized oysters during the 4-wk treatment period except taurine in the adductor muscle (Table 9). A similar comparison, using the previously parasitized oysters after the 4-wk recovery yielded only two significant correlations with snail scale; soluble protein and hypotaurine content. In addition, lipid phosphate in the mantle tissue and fatty acid content in the adductor muscle were significantly correlated with the intensity of *Perkinsus marinus* infection after the recovery period (all recovery oysters, controls and previously parasitized, were included in the analysis, Table 9).

DISCUSSION

Oysters averaged as few as about 3 and as many as 14 snails per day during the 4-wk treatment period; however, only 11% of the oysters had 10 or more snails per day and 76% had fewer than 9 per day. This range of parasitism is typical for many reefs in the experimental area (Copano Bay-Aransas Bay, TX—White et al. 1984; Powell et al. 1987) and corresponds to the lower parasite levels used by White et al. (1988, in press) in laboratory studies on these animals.

The effects of snail parasitism were minor on a biochemical level, but substantial on an organismal level. Growth, reproductive capacity, and health, as measured by *Perkinsus marinus* infection, were significantly affected. Other odostomians also re-

TABLE 5.—Means and standard deviations for all biochemical components in mantle tissue. FAA = total of the 9 free amino acids measured; FAA- = FAA less taurine and hypotaurine; FAA– = FAA less taurine, hypotaurine, glycine, and alanine; amino acids in μmoles · mL^{-1}; other tissue components in mg · g dry wt^{-1}.

		Treatment		Recovery	
	Precontrol (n = 15) $\bar{x}$ ± SD	Control (n = 10) $\bar{x}$ ± SD	Parasitized (n = 10) $\bar{x}$ ± SD	Control (n = 6) $\bar{x}$ ± SD	Previously parasitized (n = 15) $\bar{x}$ ± SD
FAA	351 ± 94	240 ± 39	280 ± 38	294 ± 64	270 ± 64
FAA-	220 ± 67	116 ± 14	121 ± 15	134 ± 50	117 ± 43
FAA–	57 ± 18	42 ± 6	46 ± 7	49 ± 26	42 ± 13
Taurine	102 ± 33	95 ± 27	119 ± 24	108 ± 15	99 ± 21
Hypotaurine	27 ± 10	39 ± 10	50 ± 23	49 ± 10	54 ± 20
Aspartic acid	22 ± 5	15 ± 2	19 ± 3	22 ± 13	18 ± 5
Serine	8 ± 5	5 ± 2	6 ± 2	5 ± 3	5 ± 3
Threonine	3 ± 1	1 ± 0.2	1 ± 0.7	1 ± 0.4	1 ± 0.5
Glutamine	8 ± 5	2 ± 1	3 ± 0.8	4 ± 3	5 ± 3
Glutamic acid	14 ± 5	16 ± 3	18 ± 5	14 ± 5	12 ± 4
Glycine	71 ± 23	33 ± 5	38 ± 10	44 ± 31	38 ± 17
Alanine	87 ± 33	36 ± 8	38 ± 10	31 ± 10	34 ± 16
Protein	62 ± 45	28 ± 39	60 ± 57	45 ± 40	23 ± 16
Glycogen	28 ± 22	111 ± 59	66 ± 28	37 ± 13	88 ± 48
Lipid phosphate (as PO_4^{-3})	0.62 ± 0.41	0.48 ± 0.27	0.82 ± 0.39	0.5 ± 0.2	0.87 ± 0.54
Fatty acids	20.7 ± 33.1	33.2 ± 49.1	48.7 ± 58.1	9.4 ± 10.5	6.3 ± 3.2

TABLE 6.—Means and standard deviations for biochemical components of adductor muscle tissue. See Table 5 for additional information.

		Treatment		Recovery	
	Precontrol (n = 11) $\bar{x}$ ± SD	Control (n = 10) $\bar{x}$ ± SD	Parasitized (n = 10) $\bar{x}$ ± SD	Control (n = 6) $\bar{x}$ ± SD	Previously parasitized (n = 15) $\bar{x}$ ± SD
FAA	328 ± 119	306 ± 56	289 ± 47	277 ± 110	347 ± 81
FAA-	272 ± 121	227 ± 54	207 ± 35	210 ± 95	266 ± 78
FAA–	57 ± 16	57 ± 8	44 ± 5	75 ± 25	84 ± 24
Taurine	52 ± 17	53 ± 25	66 ± 25	42 ± 16	47 ± 13
Hypotaurine	8 ± 4	22 ± 7	23 ± 3	24 ± 10	33 ± 6
Aspartic acid	17 ± 7	18 ± 4	14 ± 4	18 ± 6	21 ± 8
Serine	5 ± 4	7 ± 3	5 ± 2	27 ± 21	28 ± 21
Threonine	3 ± 1	2 ± 0.9	1 ± 0.5	2 ± 1	3 ± 1
Glutamine	6 ± 2	4 ± 2	2 ± 1	6 ± 4	10 ± 8
Glutamic acid	20 ± 6	18 ± 4	21 ± 6	21 ± 4	20 ± 5
Glycine	54 ± 15	124 ± 37	119 ± 42	85 ± 54	121 ± 44
Alanine	142 ± 63	49 ± 19	39 ± 10	49 ± 30	60 ± 26
Protein	41 ± 13	49 ± 40	45 ± 56	45 ± 35	36 ± 22
Glycogen	6 ± 3	7 ± 3	6.8 ± 0.3	4 ± 2	4 ± 2
Lipid phosphate (as PO_4^{-3})	0.1 ± 0	0.2 ± 0	0.34 ± 0.3	0.25 ± 0.28	0.2 ± 0.1
Fatty acids	15.0 ± 10.0	17.5 ± 16.7	15.3 ± 24.1	6.9 ± 11.5	8.6 ± 16.9

duce host growth rate (Nishino et al. 1983). Oysters parasitized by *Boonea impressa* gained significantly less weight than nonparasitized oysters. Parasitized female oysters had significantly fewer eggs than controls (the effect on males was not quantified).

Reduced growth and impaired reproduction in the host are commonly associated with marine parasites (e.g., Menzel and Hopkins 1955; Cheng et al. 1983; Hawkes et al. 1986). Starvation produces a similar phenomenon (Fair and Sick 1982; Pipe 1985; Wright and Hetzel 1985; Devi et al. 1985). Several lines of evidence suggest that a reduction in net productivity, but not a negative energy balance, produced the results observed here. White et al. (1988) developed an energy flow model for oysters and snails. Using that model, oysters of 4 to 7 cm long, the size we used, would not incur a negative energy balance un-

TABLE 7.—Results of Duncan's multiple range test for biochemical components of the mantle and adductor muscle. Each test considered data for one biochemical component (one vertical group of 5 means) for each tissue. Different letters within a vertical group indicate significant differences at $\alpha = 0.05$ within that group.

	Protein	Glycogen	Lipid phosphate	Fatty acids		Protein	Glycogen	Lipid phosphate	Fatty acids
Mantle					Adductor muscle				
Precontrol	A	B	A	A	Precontrol	A	AB	A	A
Treatment					Treatment				
Control	B	A	A	A	Control	A	A	A	A
parasitized	AB	A	A	A	Parasitized	A	AB	A	A
Recovery					Recovery				
Control	AB	B	A	A	Control	A	B	A	A
Previously parasitized	B	A	A	A	Previously parasitized	A	B	A	A

TABLE 8.—Results of Duncan's multiple range test for free amino acids in the mantle tissue and adductor muscle. Each test considered data for one biochemical component (one vertical group of 5 means) for each tissue. Different letters within a vertical group indicate significant differences at $\alpha = 0.05$ within that group. Tau = taurine; Hyp = hypotaurine; Asp = aspartic acid; Ser = serine; Glu = glutamic acid; Gln = glutamine; Gly = glycine; Ala = alanine; FAA = total for the amino acids measured; FAA- = FAA less taurine and hypotaurine; FAA– = FAA less taurine, hypotaurine, glycine, and alanine.

	Tau	Hyp	Asp	Ser	Thr	Gln	Glu	Gly	Ala	FAA	FAA-	FAA–
Mantle												
Precontrol	A	B	A	A	A	A	AB	A	A	A	A	A
Treatment												
Control	A	A	B	A	B	B	AB	B	B	B	B	A
Parasitized	A	A	AB	A	AB	B	A	B	B	AB	B	A
Recovery												
Control	A	A	AB	A	B	AB	B	B	B	AB	B	A
Previously parasitized	A	A	AB	A	B	AB	B	B	B	B	B	A
Adductor muscle												
Precontrol	A	C	AB	B	A	A	A	C	A	A	A	BC
Treatment												
Control	A	B	AB	B	AB	A	A	AB	B	A	A	CD
Parasitized	A	B	B	B	B	A	A	AB	B	A	A	D
Recovery												
Control	A	AB	AB	A	AB	A	A	BC	B	A	A	AB
Previously parasitized	A	A	A	A	A	A	A	AB	B	A	A	A

TABLE 9.—Significant *P*-values obtained by MANCOVA from comparison of snail scale and *Perkinsus marinus* infection intensity. Tests using snail scale considered only the parasitized oysters after the treatment period and the previously parasitized oysters after the recovery period. Tests using *P. marinus* considered all oysters, controls and snail parasitized. Abbreviations same as Table 8. M = mantle tissue; A = adductor muscle; — = not significant in either tissue at $\alpha = 0.05$.

	Glycogen	Lipid phosphate (as PO_4^{-3})	Fatty acids	Tau	Hyp	Asp	Thr	Ser	Glu	Gly	Ala	FAA	FAA-	FAA–	Protein
Treatment															
Snail scale	—	—	—	0.02(A)	—	—	—	—	—	—	—	—	—	—	—
Perkinsus marinus	—	—	—	—	—	—	—	0.004(A)	—	—	—	—	—	—	—
Recovery															
Snail scale	—	—	—	—	0.04(A)	—	—	—	—	—	—	—	—	—	0.004(M)
Perkinsus marinus	—	0.03(M)	0.002(A)	—	—	—	—	—	—	—	—	—	—	—	—

til fed upon by at least 25 average-sized (1.75 mm maximum width) snails. Seven snails, a typical value in our experiments, would reduce net productivity by only 5 to 30%, on a daily basis. In addition, condition index and mantle glycogen levels increased during the treatment period in both control and parasitized oysters and the effect of snail parasitism on all biochemical components was small (oysters can regulate some biochemical components even during starvation, Swift and Ahmed 1983; but see Riley 1976).

Consequently, both reduced growth and impaired reproductive capacity can be attributed to a reduction in assimilated carbon available to the host, as a result of either a reduction in filtration rate resulting in less energy being assimilated (Ward and Langdon 1986) or the direct removal of assimilated carbon by the snail. Neither effect was permanent. Growth rate resumed and reproductive state returned to control levels during recovery. In both cases compensatory adjustments occurred during the recovery period so that previously parasitized oysters gained weight and increased egg number faster than the controls. Loosanoff and Nomejko (1955) and Eagle and Chapman (1953) also noted compensatory shell growth in oysters.

Perkinsus marinus infection is an important cause of mortality in oysters (Mackin and Sparks 1962; Mackin 1962; Hofstetter 1977). *Boonea impressa* can transmit *P. marinus* from one oyster to another and can also increase the intensity of infection (White et al. 1987). Continued deterioration after a stress is removed occurs frequently in "recovery" experiments (Kendall et al. 1984; Powell et al. 1984) demonstrating the necessity of examining recovery capacity in acute (vs. chronic) stresses. Growth rate typically recovers more rapidly than most biochemical parameters. In snail-parasitized oysters, both prevalence and intensity of *P. marinus* infection increased during the recovery period. Hence, in contrast to growth rate, no recovery from *P. marinus* actually occurred. By the end of the 8-wk period, infection intensity had increased by about 1 unit on Mackin's (1962) 5 point scale. Growth still occurred and reproductive capacity returned to control levels, however, during this period. These results contradict those of Menzel and Hopkins (1955) who showed that *P. marinus* retarded growth in proportion to the intensity of infection and Mackin (1953) who observed decreased fecundity in heavily infected oysters. Haven (1962) obtained results analogous to ours. Possibly, the oysters in our study were not infected heavily enough to retard growth and reproduction. Mean infection intensity in previously parasitized oysters after the recovery period was only 2.2, a light to moderate infection.

Changes observed at the biochemical level among the previously parasitized oysters after the recovery period, particularly in fatty acid and lipid phosphate content, were related to increased infection intensity of *P. marinus* (Table 9). Stein and Mackin (1955), Mackin (1962), and White et al. (in press) also noted changing lipid levels related to infection intensity. Lipid phosphate is predominantly a structural component whereas fatty acids, usually as triglycerides, are storage materials in many marine invertebrates (Gabbott 1976; Trider and Castell 1980; Gehron and White 1982). The increased lipid phosphate content in mantle tissue, however, probably indicates an increase in structural material, noted histologically by Stein and Mackin (1955, 1957) to occur in conjunction with *P. marinus* infections.

Glycogen is the primary storage material in most bivalves (Beninger and Lucas 1984). Parasitism frequently affects carbohydrate metabolism (Cheng 1963; Mohamed and Ishak 1981; Thompson and Binder 1984; Thompson 1986). White et al. (in press) suggested that *P. marinus* alters oyster metabolism favoring gluconeogenesis. Our results support this hypothesis. Glycogen levels dropped only in recovery control oysters in which *P. marinus* infection intensity also declined. Changing fatty acid content might be similarly explained. In contrast, Stein and Mackin (1957) noted decreased glycogen levels in heavily infected oysters (3 to 5 on Mackin's scale). Few of our oysters were this heavily infected, however. An alternative explanation, that slower reproductive development in parasitized oysters was responsible for variation in glycogen and fatty acid content, cannot be completely excluded because *P. marinus* infection intensity did not correlate with glycogen levels in recovery oysters. Parasitized oysters had fewer eggs than control oysters, however. Additionally, neither the number of eggs present nor the number of oysters spawning differed significantly between control and previously parasitized oysters during the recovery period.

Results of previous workers suggest that significant decreases in storage compounds, whether caused by *B. impressa* or *P. marinus*, only occur in heavily infected animals (e.g., Stein and Mackin 1957; White et al. in press). This, too, is true for the amino acid pool where significantly decreased levels are usually associated with more severely stressed animals (e.g., Powell et al. 1982, 1984). The few significant effects on amino acids in this study, like all the other biochemical components measured,

were produced by increases in concentration. Soniat and Koenig (1982) observed significant changes in the free amino acid pool due to *P. marinus*, particularly in taurine concentration. We noted changes in taurine during the treatment period and hypotaurine during recovery in the adductor muscle but these were related to snail parasitism.

Biochemical components, though rarely significantly affected, were affected not just in the mantle tissue but also in the adductor muscle. One possibility, that the snail's effect is localized at the point of feeding, is not supported by the data. Snail parasitism produces systemic effects.

CONCLUSIONS

Complementary results of White et al. (1984; 1988, in press) and this study permit a general description of the impact of snail parasitism on oysters at normal field levels. Both growth rate and reproductive development slow significantly, but recover rapidly once the snails are removed. Hence, the temporal stability of snail patches must determine the cumulative effect on field populations of oysters. The prevalence and intensity of infection by *Perkinsus marinus* is significantly increased, but recovery does not occur. That is, *Boonea impressa* probably facilitates and encourages the normal spread and intensification of *P. marinus* from which oysters, if they recover, only do so the following winter when low temperatures typically reduce infection levels (Hewatt and Andrews 1956; Burrell et al. 1984; Soniat 1985). This effect, then, is long term. Most changes in biochemical components were due to infection by *P. marinus*. Snail feeding reduces net productivity but, at normal field levels, starvation is an unlikely result. Increased infection by *P. marinus* typically raises glycogen and lipid levels, at least in light to moderate infections. Of the free amino acids, taurine and hypotaurine have been shown to be affected by *P. marinus* and *B. impressa*. Little change in the remaining FAA or the total pool has been observed singly or in concert. Feng et al. (1970) noted increased taurine levels in oysters parasitized by *Bucephalus* sp. and *Minchinia nelsoni*. Hence, an increase in taurine and hypotaurine levels apparently is a general response to parasitism in oysters.

Yuill (1987) emphasized the importance of subtle effects produced by parasites on host populations. *Perkinsus marinus* is an important source of mortality in oyster populations (Mackin and Sparks 1962; Mackin 1962; Hofstetter 1977). Data suggest that one of the most important aspects of parasitism by *B. impressa* is to encourage this second parasitic organism. To this extent, over the year, *B. impressa* at normal field densities could be responsible for a substantial amount of mortality in oyster populations.

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LIFE TABLES FOR TWO FIELD POPULATIONS OF SOFT-SHELL CLAM, *MYA ARENARIA*, (MOLLUSCA : PELECYPODA) FROM LONG ISLAND SOUND

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ABSTRACT

Life tables were constructed for two populations of *Mya arenaria* from Long Island Sound, USA, based on schedules of age-specific fecundity and mortality determined under natural conditions. *Mya arenaria* shows a basic conservatism in general life history pattern. In both populations, fecundity increases with increasing female size; sexual maturity is attained at 1 year of age; a single annual breeding season occurs and survivorship curves approximate the type III of Deevey, which is characterized by extremely heavy mortality early in life followed by relatively constant mortality thereafter. Differences in the age-specific parameters for the two populations exist, however; for clams greater than 1 year of age, both age-specific fecundity and survivorship are significantly higher in the Stonington population. These differences in the structure and dynamics of the two populations may be due to environmental heterogeneity. Reduced body size due to slower growth in coarse substrate, as well as the increased maintenance demands resulting from burrowing and valve activity in large-grained sediment, may account for the lower egg production and lower survival rates found in the Westport population.

The life history pattern of a species has been defined as the way in which that species partitions the limited resources of time or energy among the three basic biological processes of growth, maintenance, and reproduction. Efforts to generate empirical values for life history parameters, age-specific fecundity and survivorship, have only recently allowed the construction of life tables for field populations. Determining life history parameters for a commercially important species such as the soft-shell clam, *Mya arenaria*, is particularly useful since they can be used in theoretical models which are designed to analyze the effect of changing survival and fecundity values on the growth rate of the population.

Life tables now exist for a number of benthic marine invertebrates: the barnacle—*Chathamulus stellatus* (Connell 1961); the prosobranchs—*Dicathais orbita* (Phillips and Campbell 1974), *Nucella* (= *Thais*) *lapillus* (Frank 1969), *Nodilittorina tuberculata* (Doran 1968), and *Conus pennaceus* (Perron 1983); the coelenterates—*Muricea californica* (Grigg 1977), *M. fruticosa* (Grigg 1977), and *Balanophyllia elegans* (Fadlallah 1983); the bivalves—*Mya arenaria* (Brousseau 1978), *Tapes phillipinarum* (Yap 1977), and *Gemma gemma* (Weinberg 1985). These studies, however, examine life history parameters for a single species population or for successive cohorts within a population.

The present study examines age-specific fecundity and survivorship in two geographically separated populations of the soft-shell clam, *Mya arenaria*, using identical methodology. Since differences in methodology can influence estimates of demographic parameters (Fadlallah 1983) uniformity of approach is necessary for interpopulation comparisons. This study is the first reported examination of species-specific traits in two naturally occurring populations and was carried out as part of a broader study of the population dynamics of this species along the Connecticut shore of Long Island Sound.

MATERIALS AND METHODS

Field Study Areas

Field studies were conducted at two intertidal sites in Long Island Sound, one located at Barn Island in Stonington, CT (lat. 41°20′N; long. 71°53′W) and the other in the Saugatuck River in Westport, CT (lat. 41°06′N; long. 73°23′W) (Fig. 1). The Stonington site is a narrow intertidal sandflat which extends approximately 10 m shoreward to a coarse sand beach. At low tide the Westport site extends 30 m (at its widest point) shoreward to a *Spar-*

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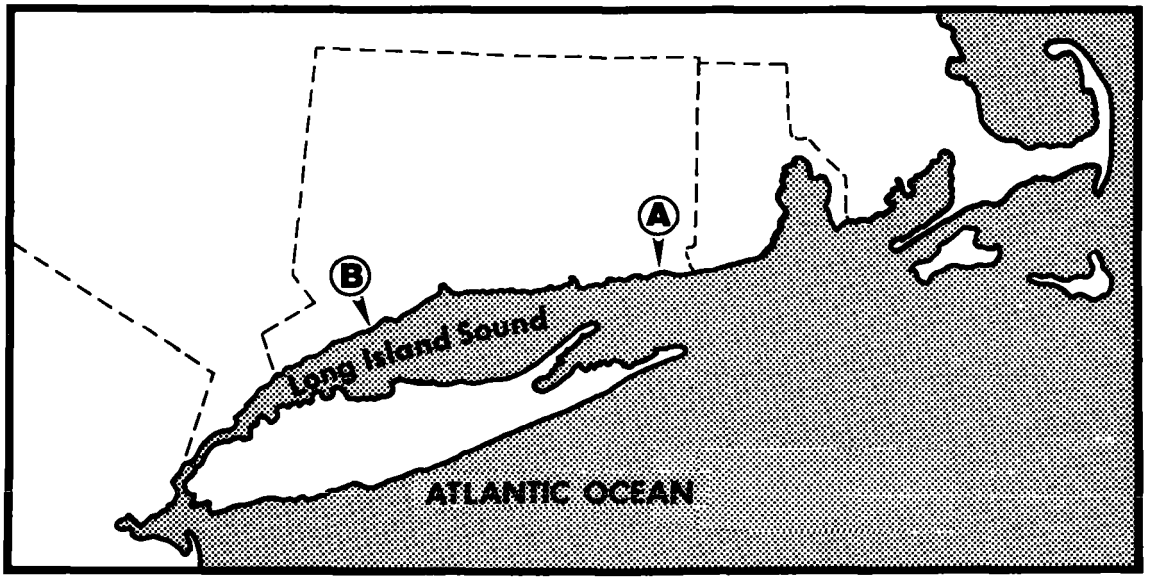


FIGURE 1.—Map showing locations of the two study sites: Barn Island in Stonington, CT (A) and Saugatuck River in Westport, CT (B).

tina alterniflora marsh. The substrate there is coarser than at the Stonington site; 50% by weight is >4 mm grain size diameter, much of that classifiable as either cobble or boulder (Brousseau and Baglivo 1987). Both study sites are closed to shellfish harvesting to high levels of bacterial contamination.

Although annual salinity and temperature profiles for the two sites are not available, monthly surface and bottom salinity and temperature readings for the period March 1979–June 1981 and October 1985–August 1986 are available for four sites in western Long Island Sound: Norwalk, CT (lat. 41°02.5′N; long. 73°27.2′W), Bridgeport, CT (lat. 41°08.7′N; long 73°11.1′W), Stratford, CT (lat. 41°07.6′N; long. 73°07.6′W), and New Haven, CT (lat. 41°14.4′N; 72°54.2′W) (Tettlebach et al., 1984; Blogoslawski, pers. comm.[3]). All water sampling was done at spring low tide in approximately 20 ft of water. The annual average range of surface temperatures for the four sites was 0.5°–24.2°C. The lowest surface temperature, 0.0°C, was recorded at the New Haven station in February 1980; the highest was 25.0°C recorded at the Stratford station in August 1986. Annual average range of bottom temperatures was 0.6°–23.4°C. Surface salinities ranged from 16.9 to 33.3‰ with a low of 15.9‰ reported for Stratford and a high of 35.7‰ recorded at the Norwalk station. Mean bottom salinities during that period ranged between 17.0 and 34.4‰.

[3]W. Blogoslawski, Northwest Fisheries Center Milford Laboratory, National Marine Fisheries Service, NOAA, Roger Avenue, Milford, CT 06460, pers. commun. March 1987.

Fecundity

Oocyte production by female clams collected during the summer spawning seasons of 1984 and 1985 was estimated using a histological technique (Brousseau 1976). One hundred twenty-five gravid females from the Westport population and 123 from the Stonington population were examined. Size-specific fecundity rates were converted to age-specific rates using age-size information for *M. arenaria* obtained from analysis of internal shell growth bands (Brousseau and Baglivo 1987). Age-specific fecundity estimates for x-yr-old clams, m_x, were calculated using the formula:

$$m_x = 0.5 \sum m_i \, P(\text{size-class } i \mid x \text{ yr-old}) \quad (1)$$

where m_i is the mean fecundity for size-class i, P(size-class i | x-yr-old) is the conditional probability that an x-yr-old clam is in size-class i, and the sum is taken over 10 mm size-classes i. The conditional probabilities P(size-class i | x-yr-old) were derived empirically (see Appendix Tables 1, 2). Ten millimeter size-classes were used because of sparseness in the data. By convention, m_x represents the

total number of eggs produced by a female of age x which may be considered to be "female eggs". Because the sex ratio of both populations is 1:1 (Brousseau 1987a), only half of the oocytes produced will eventually become females. Accordingly, each m_x is one-half the total annual fecundity per female of age x.

Mortality

To determine size-specific 1-yr survival rates of adult clams (>1 year of age), *M. arenaria* from Stonington and Westport were collected, individually tagged, and returned to their original sites (Stonington: 31 May–1 June 1985; Westport (Plot A): 1 May 1984 and Westport (Plot B): 22 May 1984). Clams were measured to the nearest 0.1 mm anteroposteriorly and marked for identification using a method described previously (Brousseau 1979). Tagged clams were replanted in parallel furrows excavated to a depth of 20–30 cm. All plots were 0.3 m apart and located at midtide level (+3.0 m). At the end of the test period, the clams were collected. All numbered individuals, both alive and dead, were returned to the laboratory for measurement. A total of 1,049 clams from the Stonington population were tagged, of which 78% were recovered. One-year recovery rate at the Westport site was 40% of the 1,977 clams initially planted. Mortality rates were determined on the basis of the number of clams recovered. This method gives a more accurate estimate of mortality since it does not consider clams that were not recaptured in these estimates.

If, on recapture, a dead clam showed no evidence of growth, either death had occurred naturally in a slow-growing individual or premature death had occurred as a result of trauma due to the marking procedure. In order to correct for premature mortality caused by handling, the proportion of live clams which showed an increase in shell length over the year was calculated (Table 1). For the Westport population all live clams <40 mm shell length grew, while 94.7% of live clams over 40 mm grew. For the Stonington population all live clams <50 mm shell length had grown during the year, while 91.9% of live clams over 50 mm grew. In order to estimate size-specific survivorship then, the following rules were applied:

TABLE 1.—Distribution of *Mya arenaria* recovered alive showing growth and no growth during the test period.

	Westport (clams >40 mm)		Stonington (clams >50 mm)	
	Growth	No growth	Growth	No growth
Number	196	11	440	39
Percent	94.7	5.3	91.9	8.1

Westport:

Classes <40 mm: P(surviving one year) $= N_A/(N_A + N_{DG})$ (2)

Classes >40 mm: P(surviving one year) $= N_A/(N_A + N_{DG}/0.947)$

Stonington:

Classes <50 mm: P(surviving one year) $= N_A/(N_A + N_{DG})$ (3)

Classes >50 mm: P(surviving one year) $= N_A/(N_A + N_{DG}/0.919)$

where N_A is the number alive and N_{DG} is the number dead with growth. In the smaller classes (Westport, <40 mm; Stonington, <50 mm), the sum $N_A + N_{DG}$ represents all recovered individuals, while in the larger classes, the adjustment factor allows us to add a number of dead without growth back into the total recovered in the same proportion as the live with no growth.

Age-specific survival rates, P_x, were based on the same age-size information used to determine age-specific fecundity rates. These rates were calculated using the formula:

$$P_x = \sum p_i \, P(\text{size-class } i \mid x\text{-yr-old}) \quad (4)$$

where p_i is the probability that a clam in size-class i survives one year, P(size-class i | x-yr-old) is the conditional probability that an x-yr-old clam is in size-class i, and the sum is taken over 10 mm size classes i.

The probability of surviving from settlement to one year (a period of about 10 months) is calculated from the estimates of the density of the population in 2 consecutive years. Both populations were sampled during periods of maximum settlement in 1985. This period occurred approximately 3 weeks earlier in the Westport population. At each sampling, 18 to 35 samples (0.1 m^2 × 30 cm deep) were taken along transects running from mean low water shoreward to the mean high water mark. Samples were wet-seived in the laboratory (2 mm mesh) and the shell lengths of the clams retained by the seive were measured. Clams of size 2–20 mm in the first year of sampling are assumed to be the spat; those of size 20–50 mm the following year are assumed to have come proportionately from the settlement of the previous year in the same ratios as the empirical probability distributions (Appendix Tables 1, 2).

RESULTS

Fecundity

Fecundity of *Mya arenaria* increased with increasing female body size (Fig. 2). Size-specific fecundity schedules, however, differed at the two study sites. Comparison of regression lines for log(fecundity) vs. shell length by analysis of covariance indicated that the relationships were significantly different ($P = 0.004$). Size-specific oocyte production in the Stonington clams was larger than in clams from Westport. The smallest gravid females observed were 34 and 27 mm in shell length in the Stonington and Westport populations, respectively. Age at first reproduction is 1 year in clams from both sites. Sex ratios in both populations did not differ significantly from 1:1 (Brousseau 1987a).

Recruitment and Mortality

Both temporal and spatial variations in annual recruitment were observed during the study period. A substantial settlement occurred at the Westport site in 1985, as evidenced by the high densities of 2–20 mm clams present in late July of that year (Table 2). In contrast, spat densities at the Stonington site were low in early August of 1985, when settlement occurred. Nonetheless, persistence of the 1985 year class at Westport was poor, whereas approximately one-half of those set in the Stonington population during that year were alive one year later. The coarse substrate at the Westport site may have aided attachment of the byssal stage juveniles, resulting in the higher recruitment rate during the summer of 1985. Direct estimates of *M. arenaria* survivorship during the postsettlement to 1-yr

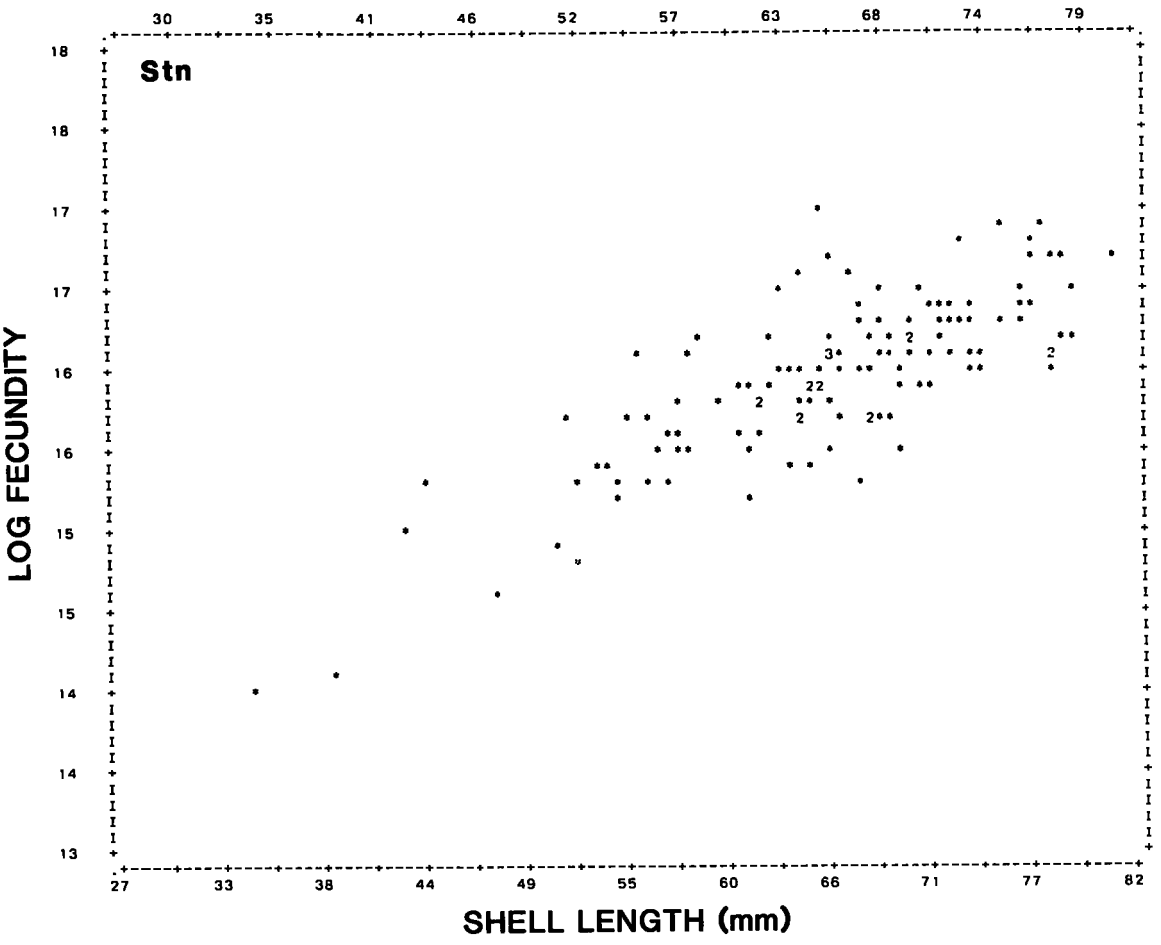


FIGURE 2.—Log of fecundity versus shell length for *Mya arenaria* from

TABLE 2.—Densities per 0.1 m^2 of *Mya arenaria* in size-classes 2–50 mm in the Westport and 2–60 mm in the Stonington populations in 1985 and 1986.

Location and date	Samples	Size-class (mm)	*N*/0.1 m^2	(range)
Westport, Connecticut				
23 July 1985	28	2–20	23.36	(0–84)
09 June 1986	18	10–20	0.11	(0–1)
		20–30	0.44	(0–5)
		30–40	0.89	(0–4)
		40–50	0.50	(0–3)
Stonington, Connecticut				
15 Aug. 1985	35	2–20	0.37	(0–7)
24 June 1986	24	20–30	0.04	(0–1)
		30–40	0.13	(0–1)
		40–50	0.33	(0–2)
		50–60	0.75	(0–3)

period (10 months) obtained by dividing the number of 1-yr-olds alive in the summer 1986 by the estimated cohort size in the previous year were 0.0283 and 0.5869 for the Westport and Stonington populations, respectively.

Size-specific survival rates of adult clams (≥1 year) at both sites are shown in Tables 3 and 4. These represent empirical estimates from mark and recapture studies with survival adjustments in the larger classes made according to Equations (2) and (3). Statistical comparison of the survival distributions of adult clams, however, was limited to those recovered live or recovered showing some growth. At the Westport site survival was constant across the 10 mm size classes: 20–29 through 50–59 and 60+. At Stonington, however, the size-specific survival for classes 30–39 through 70–79 and 80+ increased slightly with size ($P < 0.05$, χ^2 test). The probability

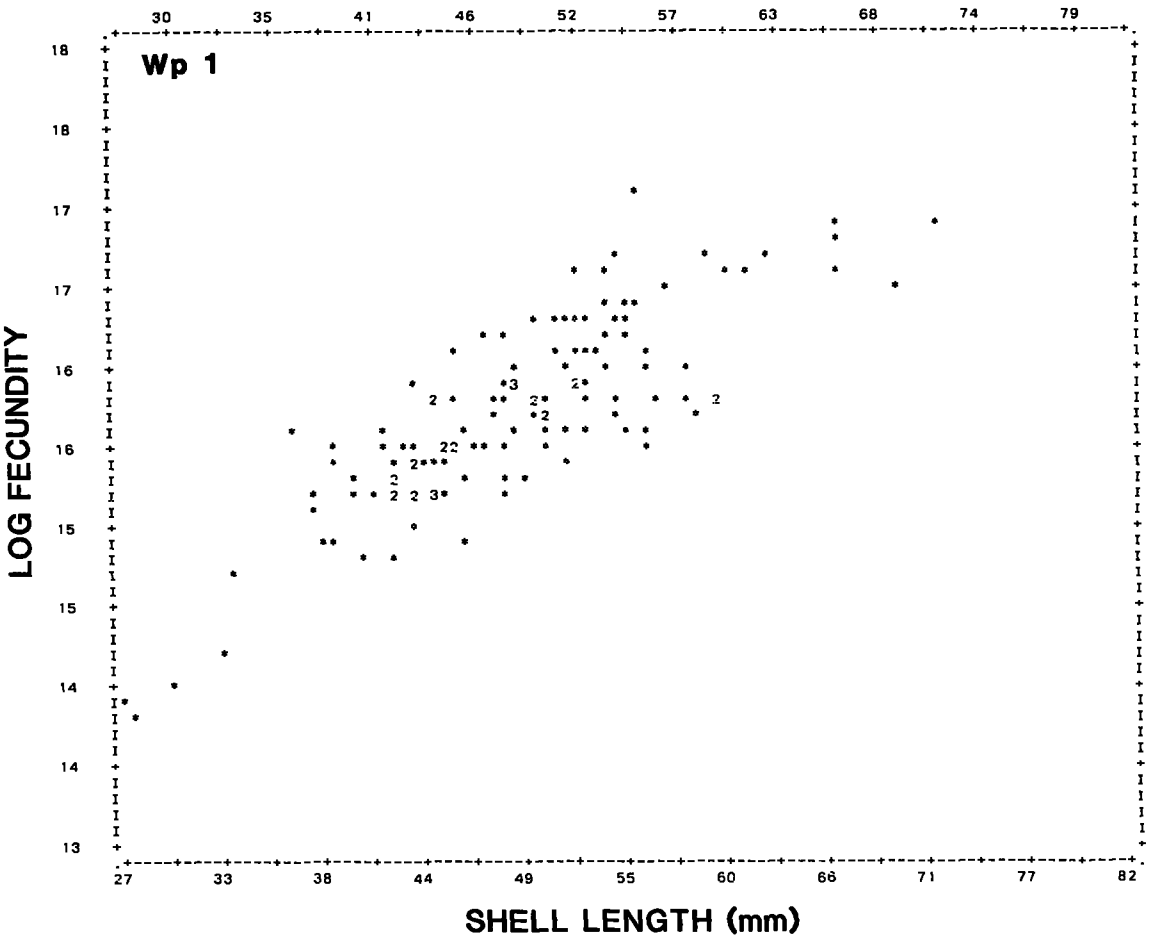


FIGURE 2.—*Continued*—the Stonington (STN) and Westport (WP1) populations.

TABLE 3.—Size-specific survival rates for marked *Mya arenaria* from the Stonington population. P = probability of an individual from size-class i surviving one year; N_A = number of live clams; N_{DG} = number of dead clams showing growth.

Size-class	Size (mm)	N_A	N_{DG}	P
2	20–30			
3	30–40	23	3	0.8846
4	40–50	106	18	0.8548
5	50–60	134	7	0.9462
6	60–70	161	11	0.9308
7	70–80	159	9	0.9420
8	80+	25	0	1.0000

TABLE 4.—Size-specific survival rates for marked *Mya arenaria* from the Westport population. P = probability of an individual from size-class i surviving one year; N_A = number of live clams; N_{DG} = number of dead clams showing growth.

Size-class	Size (mm)	N_A	N_{DG}	P
2	20–30	15	5	0.7500
3	30–40	87	56	0.6084
4	40–50	150	76	0.6515
5	50–60	48	19	0.7052
6	60–70	9	5	0.6303
7	70–80	0	0	0.0000
8	80+			

of surviving one year for adult clams at Stonington (30+ mm in shell length) is significantly higher than at Westport (20+ mm in shell length) ($P < 0.001$, χ^2 test).

Age-specific survivorship estimates (Table 5) were calculated by assuming that 20–30 mm clams at Stonington survivied with the same probability as 30–40 mm clams and that 90–100 mm clams at Stonington survived with the same probability as 80–90 mm clams and application of Equation (4) using the empirical distributions in Appendix Tables 1 and 2.

TABLE 5.—Age-specific survival rates for marked *Mya arenaria* from the Westport and Stonington, CT populations. P_x = probability of surviving from age-class x to age-class $x + 1$.

Age-class (yr)	Westport P_x	Stonington P_x
1	0.6390	0.8843
2	0.6442	0.9307
3	0.6625	0.9390
4	0.6680	0.9550
5	0.6595	0.9661
6	0.6422	0.9746
7	0.6128	0.9746
8	0.5991	0.9746
9	0.5021	0.9746

Population Dynamics

The age-specific survivorship and fecundity schedules for *M. arenaria* are combined in life table form in Tables 6 and 7. Since rates of larval survivorship are difficult to measure for species with planktonic larvae, simplifying assumptions are necessary for estimating survivorship probabilities of larvae (age 0). In order to complete the life tables the equilibrium settlement rates (r_s) were calculated using the method of Brousseau et al. (1982). Our choice of r_s implies that the net reproductive rate, R_0, which is defined by $R_0 = \sum l_x m_x$, were l_x = survivorship and m_x = fecundity, equals one for both populations. This is not meant to imply however, that the populations studied here are considered to be in equilibrium. Rather, it is used simply as a theoretical construct in which to examine possible consequences of differing fecundity and mortality schedules on the two populations of *M. arenaria*.

TABLE 6.—Life table for the Westport, CT *Mya arenaria* population, assuming equilibrium conditions. l_x = survivorship to beginning of age interval x, or $l_{x-1} \times P_{x-1}$ when $x > 1$; m_x = fecundity during age interval x.

Age (yr)	l_x	m_x	$l_x m_x$
0	1.0		
1	[1]1.0599 × 10^{-7}	1485615	0.1575
2	6.7728 × 10^{-8}	2989512	0.2025
3	4.3630 × 10^{-8}	3867846	0.1688
4	2.8905 × 10^{-8}	5192053	0.1501
5	1.9309 × 10^{-8}	5892286	0.1138
6	1.2734 × 10^{-8}	6464925	0.0823
7	8.1780 × 10^{-9}	6478050	0.0530
8	5.0115 × 10^{-9}	6842903	0.0343
9	3.0024 × 10^{-9}	8390977	0.0252
10	1.5075 × 10^{-9}	8390977	0.0126

[1] $l_1 = r_s \times$ (probability of surviving from 2 months to 1 year).

TABLE 7.—Life table for the Stonington, CT *Mya arenaria* population, assuming equilibrium conditions. l_x = survivorship to beginning of age interval x, or $l_{x-1} \times P_{x-1}$ when $x > 1$; m_x = fecundity during age interval x.

Age (yr)	l_x	m_x	$l_x m_x$
0	1.0		
1	[1]2.014 × 10^{-8}	1109952	0.0224
2	1.7811 × 10^{-8}	3712746	0.0661
3	1.6577 × 10^{-8}	4947569	0.0820
4	1.5566 × 10^{-8}	7125027	0.1109
5	1.4866 × 10^{-8}	8287563	0.1232
6	1.4362 × 10^{-8}	8724158	0.1253
7	1.3997 × 10^{-8}	8724158	0.1221
8	1.3642 × 10^{-8}	8724158	0.1190
9	1.3296 × 10^{-8}	8724158	0.1160
10	1.2958 × 10^{-8}	8724158	0.1130

[1] $l_1 = r_s \times$ (probability of surviving from 2 months to 1 year).

The equilibrium settlement rate (r_s) for the Westport population is 3.7453×10^{-6} and that for the Stonington population is 3.4318×10^{-8}. The equilibrium first year survival rates (i.e., the probability of surviving from egg to year 1 necessary to maintain a population at equilibrium) then, become 1.0599×10^{-7} and 2.014×10^{-8} for the Westport and Stonington populations, respectively.

Under the assumption of equal rates of larval import and export, it is possible to calculate empirical settlement rates by estimating the total number of eggs released per unit area by spawning females in 1985 and dividing this value into the densities of 2–20 mm spat settled per unit area 2 months later. Size-frequency data for the populations was used to determine the number of clams in each 10 mm size class (Fig. 3). The number of animals in each class (assuming that one-half the population is female) was multiplied by the mean size-specific annual fecundity value for that size class. Summing over all size classes of reproducing females gives an estimate of the 1985 oocyte production per unit area. Empirical settlement rates of 8.4589×10^{-6} and 7.1953×10^{-8} were calculated for the Westport and Stonington populations. These represent values of 2.2585 and 2.0967 times the estimated equilibrium settlement rate of these populations. Multiplying the empirical settlement rate by the probability of surviving the remainder of the year give actual first year actual first year survival rates of 2.3939×10^{-7} and 4.2229×10^{-8} for Westport and Stonington, respectively.

The heavy mortality evident by the low juvenile survivorship rates (l_1) for *M. arenaria* take into account the losses incurred during fertilization, metamorphosis and recruitment, and subsequent survival through the first year of life. Table 8 compares the first year survival rates of representative marine invertebrate species with planktonic and nonplanktonic modes of development. Early survival in species lacking planktonic larvae is on average, three orders of magnitude higher than that of species which pass through a planktonic larval stage.

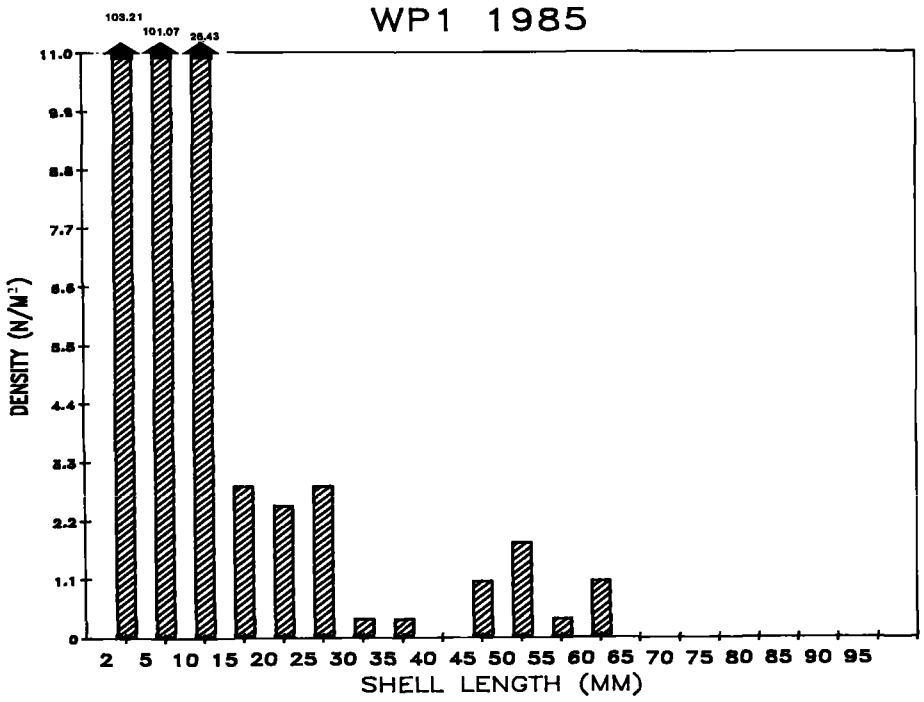
DISCUSSION

General comparisons of life history traits are useful but quantitative comparisons are possible only from the more detailed information found in life tables (age-specific fecundity and survivorship). The difficulty in generating such information, especially for marine bivalves, many of which have planktonic larval stages during their life cycles, has resulted in the construction of few complete life tables. Moreover, no reported field study has examined life history traits for more than one population of a species simultaneously. Consequently, the extent to which quantitative differences in life history parameters are characteristic of the life history of a single species is unknown.

TABLE 8.—Empirical estimates of first year survival rates of marine invertebrate species with and without planktonic larvae (adapted from Perron 1983).

Class	Species	Survivorship l_1	Developmental mode	References
Anthozoa	*Muricea californica*	2.6×10^{-7}	planktonic	Grigg (1977)
	Muricea fruticosa	3.7×10^{-6}	planktonic	Grigg (1977)
	Balanophyllia elegans	5.0×10^{-2}	nonplanktonic	Fadlallah (1983)
Bivalvia	*Gemma gemma*		nonplanktonic	Weinberg (1985)
	Cohorts 1978–1981	2.3×10^{-2}		
		1.2×10^{-1}		
		2.0×10^{-1}		
		1.1×10^{-1}		
	Mya arenaria		planktonic	Present study
	Westport population	$2.4 = 10^{-7}$		
	Stonington population	4.2×10^{-8}		
	Tapes phillipinarum	1.8×10^{-6}	planktonic	Yap (1977)
Gastropoda	*Thais lamellosa*	[1]9.0×10^{-3}	nonplanktonic	Spight (1975)
	Conus pennaceus	7.0×10^{-4}	nonplanktonic	Perron (1983)
	Lacuna pallidula	2.0×10^{-4}	nonplanktonic	Smith (1973)
	Aplysia juliana	[2]8.4×10^{-7}	planktonic	Sarver (1979)
Crustacea	*Balanus glandula*	6.0×10^{-5}	planktonic	Connell (1970)
	Barnacles (3 spp.)	2.0×10^{-5}	planktonic	Hines (1979)

[1]Does not include prehatching mortality.
[2]Survival through 30-d planktonic period only.



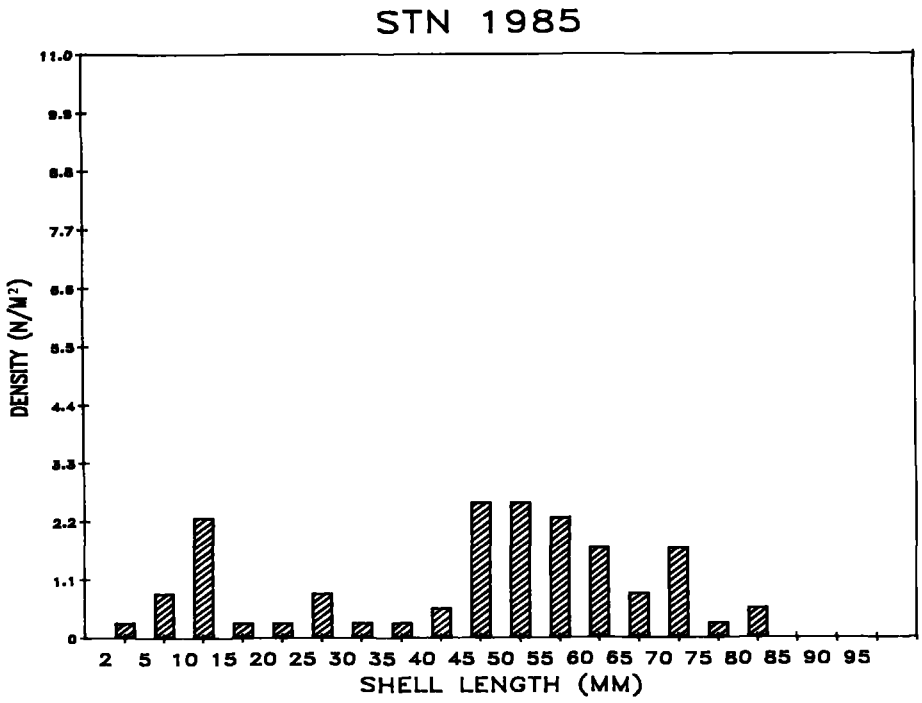
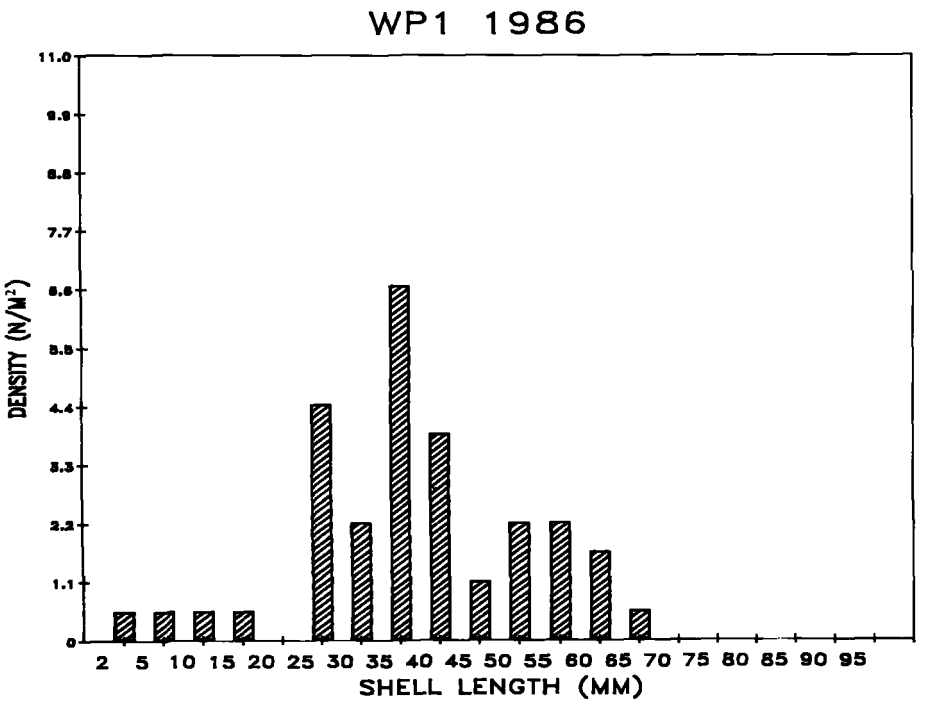


FIGURE 3.—Size-frequency distributions of *Mya arenaria* from the Stonington (STN)



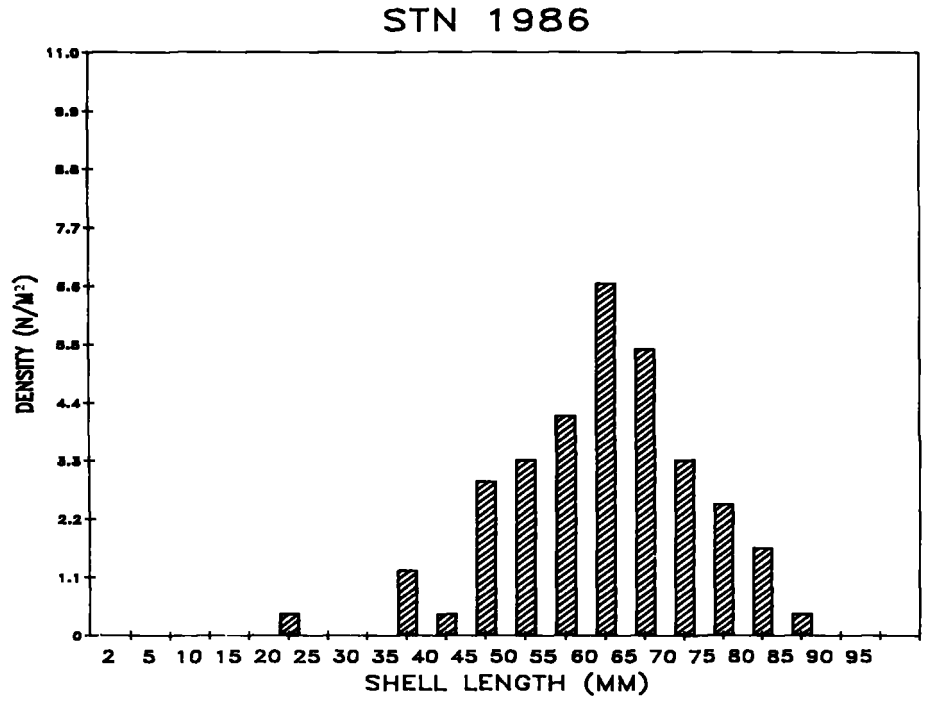


FIGURE 3.—*Continued*—and Westport (WP1) populations in 1985 and 1986.

The two populations of *M. arenaria* from Long Island Sound appear to show a basic conservatism in general life history pattern. In both populations, fecundity increases rapidly in young females with individuals reaching sexual maturity in time to reproduce at the beginning of their second year of life. Similarly, larval and adult survivorship schedules follow the type III survivorship curve of Deevey (1947). Extremely heavy mortality early in life is followed by roughly constant mortality thereafter. This pattern is similar to that described for a population of *M. arenaria* from Gloucester, MA (Brousseau 1978) except that in the latter, age of first reproduction occurs at the end of the second year. It is interesting to note, however, that some of the major life history features of *M. arenaria* show considerable latitudinal variation within the species. Frequencies of spawnings during the year increases (for review see Ropes and Stickney 1965; Brousseau 1987a) and length of life and body size show a tendency to decrease with decreasing latitude (Belding 1930; Newcombe 1935). Details of the ways in which such variations affect the life history parameters, however, remain to be studied.

The possibility of gene flow between populations of animals with planktonic larval stages always exists. Nevertheless, the amount of genetic overlap is effectively reduced as the geographical distance between the populations increases. The significant quantitative differences in the age-specific demographic parameters for the two populations studied here suggest that within the framework of a general life history strategy, a response to the biotic and abiotic components of the immediate environment is possible. Evidence from this study indicates that environmental conditions at the Westport site may be less optimal for the growth and maintenance of *M. arenaria* than are those at the Stonington site. The higher equilibrium settlement rate calculated for the Westport population indicates that on average, a larger annual spatfall is needed to maintain that population than is required at the Stonington site.

The biotic factors most often cited as agents capable of altering the survival and fecundity of individuals are predation, competition, disease, and parasitism. It is unlikely that predation was a major source of adult mortality at either site for reasons previously discussed. Moreover, the effects of predation would be limited to the small, surface-dwelling clams, since 1) crabs, fish, and birds are unable to capture deep burrowing adults and 2) it has been demonstrated that *M. arenaria* exhibits a "size refuge" from naticid predators (Edwards and Huebner 1977). Hancock (1973) has suggested that competition for food or space between the spat and adults may contribute to lowered survival in newly settled clams. If this were the case, one would expect lower juvenile survivorship rates in the Stonington population where population densities were greater (Fig. 3).

Trematode infestations have been demonstrated to cause castration and high mortalities in a population of venerid clams, *Transenella tantilla*, in California (Obrebski 1968). Although both trematode infections (Stunkard 1938; Uzmann 1951) and fungal parasites have been reported in *M. arenaria* (Andrews 1954), no evidence of either was observed in the 2,826 histologically prepared clams (1,583 from Stonington; 1,243 from Westport) examined in a study of the reproductive cycle in the two populations (Brousseau 1987a). Sarcomatous neoplasia, a proliferative disorder characterized by increased number of "leukemia-like" cells in the tissues and organs (Farley 1969; Brown et al. 1977; Cooper et al. 1982), has been identified in samples of clams from both Stonington and Westport. Prevalence of the disorder in the Stonington population ranges from 0 to 46%, whereas 0–69% of the *M. arenaria* from Westport were neoplastic, depending on the collection date (Brousseau 1987b). At present it is not known if neoplasia is a source of mortality in field populations of clams. It seems reasonable to assume that it is, however, since neoplastic cells are invasive and at times cause the destruction of organs and tissues in infected animals (Yevich and Barszcz 1977). If sarcomatous neoplasms prove to be malignant, this disease could be responsible to some degree for the higher mortality rates reported in the Westport population.

The abiotic factors with the greatest effect on the biotic potential of estuarine organisms are temperature, salinity, substrate, and food availability. Adult *M. arenaria* typically inhabit the intertidal zone and are adapted to a wide range of fluctuations in water temperature and salinity. In addition, sediments tend to buffer temperature and salinity fluctuations (Sanders et al. 1965; Johnson 1965, 1967). Therefore, infaunal organisms like the soft-shell clam are subject to less extreme environmental fluctuations than are exposed organisms living on or attached to the surface. Belding (1930) noted that *M. arenaria* withstands extreme variation in salinity, being able to adjust to changing tides every six hours. Shaw and Hamons (1974) found that lethal conditions for burrowed clams were met only when temperatures persisted in the high 20°C range and salinities were 2‰ or lower. In the laboratory,

adult survival is not altered by salinities of 2.5‰ (Chanley 1957; Pfitzenmeyer and Drobeck 1963; Castagna and Chanley 1973) to 35‰ (Castagna and Chanley 1973). Annual water temperature and salinity patterns in Long Island Sound fall well within the range of conditions tolerated by *M. arenaria* (see Materials and Methods). If temperature and salinity differences did occur, their effects would be minimal.

Substrate differences at the Stonington and Westport sites appear to be the most immediate cause of the observed differences in age-specific fecundity and survivorship. Several investigators have found that sediment type is important in controlling growth rate and shell allometry in *M. arenaria* (Belding 1930; Swan 1952; Newell and Hidu 1982). Clams grown on coarse sediments (gravel, cobble), such as that at the Westport site are slow-growing and more globose in shape than clams from sand or mud environments. Although differences in growth rate could be due to differences in food availability at the two sites, the allometric variations (Brousseau and Baglivo 1987) strongly support the hypothesis that substrate effect is the factor controlling growth. Reduced body size in Westport clams may have an indirect effect on fecundity by restricting egg production. In addition, both Glude (1954) and Pfitzenmeyer and Drobeck (1967) demonstrated that *M. arenaria* burrows fastest in fine-grained sediments since physical resistance to burrowing increases with increasing particle size (Trueman 1954). Hence, the high daily maintenance requirements of Westport clams may result in less energy available for reproduction, long-term maintenance, and survival. The Westport population may be an example of a population inhabiting a marginal environment.

The underlying pattern of life history (reproductive effort, patterns of recruitment, survival profile, and growth schedule) for both populations of *M. arenaria* is very similar. This is not surprising since population parameters are viewed as evolved, species-specific traits. Nevertheless, our evidence for local differentiation in different habitats demonstrates the degree to which individual populations of a widespread species can respond in different ways to their immediate environments; environmental heterogeneity can be reflected in the structures and dynamics of local populations.

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APPENDIX

APPENDIX TABLE 1.—Empirical distributions for age-size relationships for the Westport, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)								
	1	2	3	4	5	6	7	8	9+
10–20	1 (3.8)								
20–30	9 (34.6)	3 (2.0)							
30–40	13 (50.0)	55 (37.2)	19 (12.7)	2 (2.9)					
40–50	3 (11.5)	70 (47.3)	65 (43.3)	15 (21.4)	7 (15.6)	4 (8.7)	3 (8.3)	3 (7.9)	
50–60		19 (12.8)	60 (40.0)	40 (57.1)	24 (53.3)	23 (50.0)	16 (44.4)	17 (44.7)	6 (23.1)
60–70		1 (0.7)	5 (3.3)	12 (17.1)	13 (28.9)	17 (37.0)	14 (38.9)	14 (36.8)	14 (53.8)
70–80				1 (1.4)	1 (2.2)	2 (4.3)	2 (5.6)	4 (10.5)	6 (23.1)
80–90							1 (2.8)		

APPENDIX TABLE 2.—Empirical distributions for age-size relationships in the Stonington, CT *Mya arenaria* population. Percentage in each size category per age are indicated in parentheses.

Size (mm)	Age (yr)					
	1	2	3	4	5	6+
20–30	15 (26.8)					
30–40	22 (39.3)	4 (5.1)				
40–50	13 (23.2)	5 (6.4)	2 (1.1)			
50–60	6 (10.7)	31 (39.7)	37 (20.2)	5 (3.8)		1 (7.1)
60–70		31 (39.7)	94 (51.4)	26 (19.8)	2 (7.1)	1 (7.1)
70–80		7 (9.0)	41 (22.4)	66 (50.4)	14 (50.0)	4 (28.6)
80–90			9 (4.9)	31 (23.7)	11 (39.3)	6 (42.9)
90–100				3 (2.3)	1 (3.6)	2 (14.3)

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A LONG-TERM STUDY OF "MICROCELL" DISEASE IN OYSTERS WITH A DESCRIPTION OF A NEW GENUS, *MIKROCYTOS* (G. N.), AND TWO NEW SPECIES, *MIKROCYTOS MACKINI* (SP. N.) AND *MIKROCYTOS ROUGHLEYI* (SP. N.)

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ABSTRACT

Continuing long-term studies of oyster disease problems have been carried out over the past 26 years using field monitoring, gross, histologic, and ultrastructural pathologic methods.

A microorganism of uncertain taxonomy was discovered in 1963 by J. G. Mackin in association with lesions and mortalities of Japanese oysters, *Crassostrea gigas*, from Denman Island, British Columbia, Canada. Mackin coined the term "microcell" for this organism and described the parasite as 1–3 μm cells with small nuclei which occurred within vesicular connective tissue cells adjacent to characteristic abscesses. We are describing this organism as *Mikrocytos mackini* sp. n. in his honor. Similar appearing organisms were seen by the senior author in flat oysters, *Ostrea edulis*, from Milford, Connecticut, on three different occasions: 1) in oysters transferred from Milford, Connecticut, to Chincoteague Bay, Virginia; 2) in oysters transferred from Milford to Elkhorn Slough, California; and 3) in oysters transferred from Milford to Oxford, Maryland, and held in recirculated sea water. The causative organism in these three episodes has been shown by electron microscopy to be *Bonamia ostreae*, the parasite that was implicated in recent mortalities in flat oysters in Europe. Similar organisms have also been seen in Olympia oysters, *Ostrea lurida*, from Oregon and in the Sydney rock oyster, *Saccostrea commercialis*, from Australia. Presence of the organism in the latter species is associated with the winter mortalities originally described by T. C. Roughley, and the pathogen is here described as *Mikrocytos roughleyi* (sp. n.) in his honor.

"Microcell" type parasites of oysters are associated with a complex of diseases that occur in Japanese oyster, *Crassostrea gigas*; Sydney rock oyster, *Saccostrea commercialis*; flat oyster, *Ostrea edulis*; and Olympia oyster, *O. lurida*, in North America, Europe, and Australia. Severity of disease varies from an acute, highly lethal form to a chronic, seasonally recurring disease that does not produce massive mortalities. The etiologic agents are small, morphologically simple, and very difficult to compare and characterize taxonomically at light microscope levels of resolution. Associated lesions vary according to species affected and provide some of the differences that may be used to distinguish the agents involved. The complexity of this group and the difficulties involved in achieving an understanding regarding whether we are dealing with one or a group of organisms and how they were transferred to new locations, the long time span involved in answering these questions, and the continuing dissemination of unpublished privileged information shared in informal workshop gatherings of scientists with common interests, make it necessary to use unpublished anecdotal information in order to provide as complete a story as possible.

The first oyster mortality known to be associated with "microcell" disease was reported in *C. gigas* from Denman Island, British Columbia, Canada by Quayle (1961). Quayle's report documents the epizootic aspects from 1956 to 1960 and demonstrates the gross appearance of the disease in the Pacific oyster. A causative agent was not identified until several years later, when the late J. G. Mackin[4] (unpubl. data) discovered a small intracellular organism intimately associated histologically with tissue abscesses in diseased oysters (*C. gigas*) from Denman Island and called this organism "microcell". He demonstrated this material at the 1963 Shellfish Mortality Conference held at Oxford, MD.

Mackin's demonstration provided us with the insight to identify similar organisms in histologic sec-

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tions of Denman Island oysters in our laboratory collection and further led to the discovery of microcell disease in *O. edulis*, *O. lurida*, and *S. commercialis* from Australia ("Australian winter disease") described by Roughley (1926). In 1979, the characteristics of microcell disease were demonstrated at a microscopic diagnosis workshop held at the Ministry of Agriculture and Fisheries Laboratory in Weymouth, England. This workshop was attended by molluscan pathologists from several European countries including France. In the late 1970s, serious mortalities of *O. edulis* in France, associated with microcell infections, were described in a paper by Pichot et al. (1979), in which the organism was named *Bonamia ostreae*. Reference to the earlier work on microcell by Mackin and others (Katkansky et al. 1969) was not included in their report.

Since the taxonomic relationship and status of these similar parasites have not been described, it is the purpose of this paper to present a complete background on microcell related epizootics and morphological information which, in North America, preceded the French report (Pichot et al. 1979). Furthermore, microscopic and ultrastructural comparisons of the microorganisms are provided and a new genus, *Mikrocytos* g. n., and two new species, *Mikrocytos mackini* sp. n. and *Mikrocytos roughleyi* sp. n., are described.

MATERIALS AND METHODS

General Procedures

Oyster tissues were collected from a variety of sources as follows:

Code WWC were *C. gigas* collected from Henry Bay, Denman Island, British Columbia, Canada on a periodic basis from April 1968 to June 1969 by D. B. Quayle (spring 1969 samples were collected by N. Bourne). Live oysters were sent by air freight to the Oxford Laboratory where clinical and gross features were recorded and they were processed for histological and, in some cases, ultrastructural studies.

Code S-124-A were *C. gigas* from Hawaii collected in September 1972.

Code S-41 were *S. commercialis* collected by Peter Wolf from 22 July to 23 July 1965 from the Georges River, Woolooware Bay, New South Wales and shipped to the Oxford Laboratory for processing.

Code FK were progeny of *O. edulis* from Boothbay Harbor, ME that were spawned at Milford, CT in April 1961. Seed oysters were transplanted to Chincoteague Bay, VA in May 1961 and processed at subsequent intervals (FK-1-1 to FK-2-5, August 1961; FK-3-1, August 1961; FK-4-1 and FK-4-2, February 1962).

Code WAC were *O. edulis* bred in the Milford, CT hatchery from 1963 to 1965, and introduced into California bays as follows:

WAC-1, Milford 1963 seed oysters planted in Morro Bay, CA in December 1964 and sampled on 7 December 1965 during a heavy mortality.

Sample WAC-21-28 consisted of 38 oysters from a Milford 1963 stock shipped to California in 1964 and held at Pigeon Point Laboratory, Pigeon Point, CA until heavy mortality occurred and sampled on 11 May 1966.

WAC-3-1-10 were 1963 Milford oysters placed in Morro Bay in 1964. Heavy mortality was noted and samples were taken. WAC-3-11-15 were 1963 Milford stock placed in Morro Bay in 1964. Mortality was low. Oysters were necropsied and fixed on 1 May 1966. WAC-3-16-26 were Milford 1962 stock placed in Morro Bay in 1963. They experienced 40% mortality and were examined and fixed on 1 May 1966. Oysters WAC-4-1 through 4-5 were from Milford 1963 stock placed in Tomales Bay, CA in 1964; low mortality was observed. They were examined and fixed on 1 May 1966.

Code FMT were *O. edulis* used in an experimental holding study at the Oxford Laboratory. Ten 2-yr-old *O. edulis* from the Milford hatchery were placed in each of three tanks receiving 0.45 μm membrane filtered 26‰ seawater on 23 February 1968; pH, temperature, salinity, and mortality were monitored daily until 10 October 1968. *Crassostrea virginica* from the Mispillian River, Delaware Bay, were placed in each tank on 28 March. Tanks were designated A (control), B (fed tissues of moribund *O. edulis* from Pigeon Point, CA), and C (fed tissues from Denman Island *C. gigas* infected with Denman Island disease). Seawater in each tank was recirculated through a glass wool, charcoal, calcium flow-through filter via an airlift system moving from C to B to A, respectively. Oyster codes were FMT-A-1-20, FMT-B-1-20, FMT-C-1-20, numbered as they were fixed (species were designated at time of fixation).

Code WAO-A were 50 specimen samples of native oysters (*O. lurida*) from Yaquina Bay, OR, sampled

monthly from February 1969 to January 1971. Samples were coded from WAO-7A to WAO-22A.

Tissues were fixed in Zenker's acetic, Davidson's fluid (Shaw and Battle 1957), or McDowell's fixative (McDowell and Trump 1976) as modified by Farley et al. (1986) (1% glutaraldehyde/4% formaldehyde; pH 7.2–7.4 in one-half ambient seawater). Six μm sections were stained with Harris' hematoxylin-eosin, Ziehl's fuchsin, periodic acid Schiff reagent (PAS) with malt diastase digestion, Feulgen picromethyl blue (Farley 1969), or Giemsa (Howard and Smith 1983).

Electron Microscopy Procedures

Lesions from *C. gigas* from Denman Island were fixed in 2% glutaraldehyde in pH 7.2 seawater, postfixed in 1% osmium tetroxide in phosphate buffer, pH 7.2, and embedded in Epon-Araldite (Feng et al. 1971). Fifty to 100 nm sections, selected on the basis of interference color (silver), were cut and stained with lead citrate and uranyl acetate. *Ostrea edulis* sections from the WAC material (WAC-2-19) were deparaffinized, postfixed in 2% glutaraldehyde and 1% osmium tetroxide, plastic embedded, ultrasectioned, and stained in the same fashion as the *C. gigas* materials. Sections were examined in a Zeiss[5] EM 9 electron microscope.

RESULTS

"Denman Island Disease" Studies

Table 1 presents the seasonal prevalence of gross features of samples collected in this study. Visual condition index remained high (most oysters in medium to fat condition). Mantle recession occurred most commonly from April through June and was most prevalent in June. Pale digestive gland was present in up to 24% of the oysters in the spring and was also seen in up to 16% of the oysters in fall samples. Shell pustules (Fig. 1), abscesses, and ulcers as described by Quayle (1961) (Fig. 2) were present from April through June.

Microscopical examination (Table 2) revealed granular hemocyte infiltration of vesicular connective tissue (VCT) in most samples with high prevalences of microcell infections occurring sporadically throughout the years. Abscesses (Fig. 3) in the VCT of the mantle and gonad consisted of apparently viable granular hemocytes at the periphery with phagocytosis of moribund cells deeper in the lesion and coagulative necrosis in the center. Microcell organisms were associated with these abscesses. The parasite (Fig. 4) was 1–3 μm in diameter, contained a small (1 μm) Feulgen-positive nucleus, and occurred cytozoically in VCT cells and extracellularly adjacent to and within abscesses. Microcells occurred in 60% of the abscesses found in histologic sections. However, microcells were never found outside of abscesses.

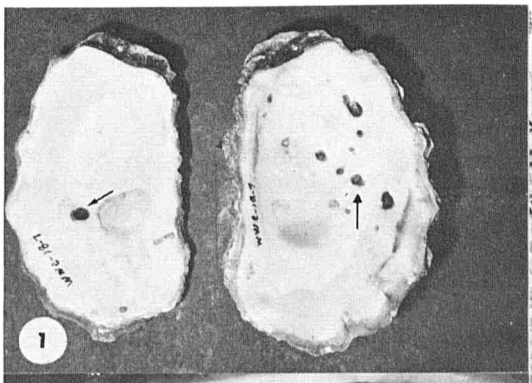
A similar disease was discovered by F. Kern[6] in *C. gigas* from Hawaii. Microcell parasites were similar in morphology and size (Figs. 5, 6) to the Denman Island organism, but infections were more

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

[6]F. G. Kern, Northeast Fisheries Center Oxford Laboratory, National Marine Fisheries Service, NOAA, Oxford, MD 21654, pers. commun.

TABLE 1.—Gross pathology in oysters from Denman Island, B.C.

Code	Date	Number in sample	% fat condition	% medium condition	% watery condition	% mantle recession	% pale digestive gland	% shell pustules	% with abscesses
WWC-1	22 May 1967	27	88	11	0	11	0	7	7
WWC-2	5 June 1967	28	100	0	0	11	7	14	7
WWC-3	10 Apr. 1968	25	88	4	8	78	24	0	16
WWC-4	22 Apr. 1968	25	100	0	0	28	0	4	12
WWC-5	24 May 1968	25	100	0	0	0	0	0	4
WWC-6	24 June 1968	25	92	8	0	8	0	4	0
WWC-7	5 Aug. 1968	25	48	48	7	8	0	0	0
WWC-8	14 Oct. 1968	25	100	0	0	0	0	0	0
WWC-9	18 Nov. 1968	25	76	24	0	0	16	0	0
WWC-10	27 Jan. 1969	25	44	56	0	0	4	0	0
WWC-11	26 Feb. 1969	18	33	61	6	0	0	0	0
WWC-12	21 Mar. 1969	25	96	7	0	0	0	0	0
WWC-13	11 Apr. 1969	25	100		0	0	4	16	16
WWC-14	12 May 1969	25	72	28	0	0	0	12	12
WWC-15	20 June 1969	25	88	12	0	12	0	4	0
WWC-18	9 June 1980	42	95	2	2	19	0	17	17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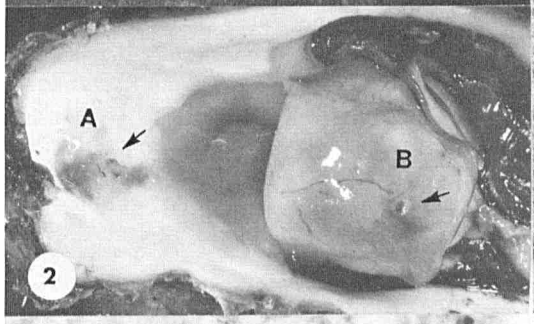
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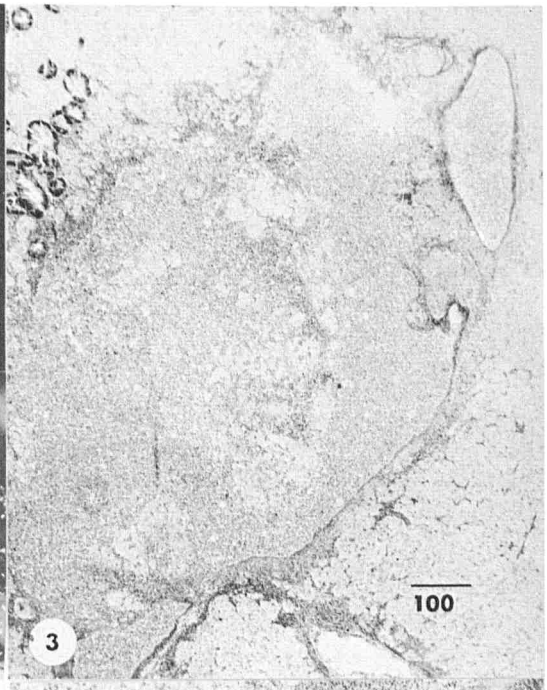
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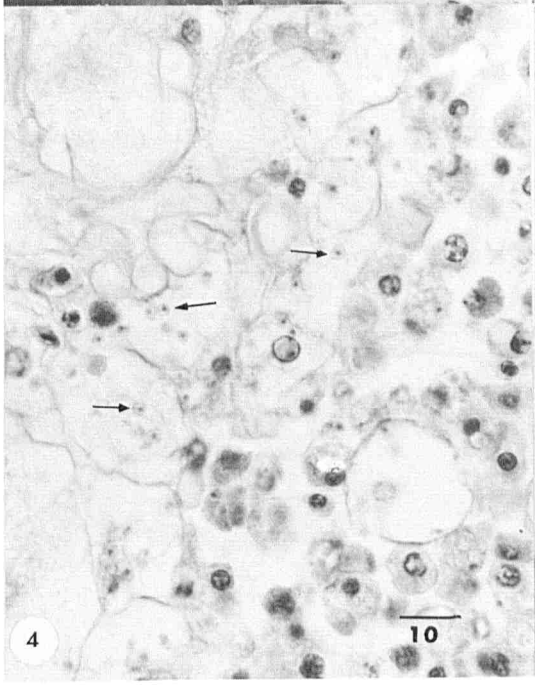
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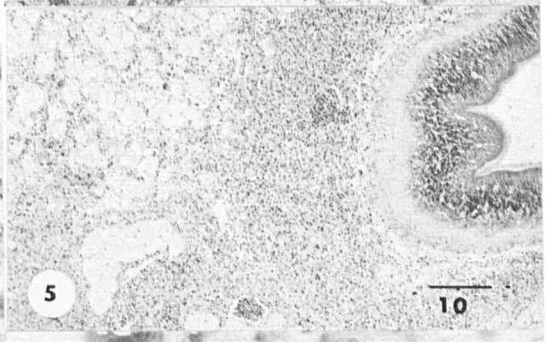
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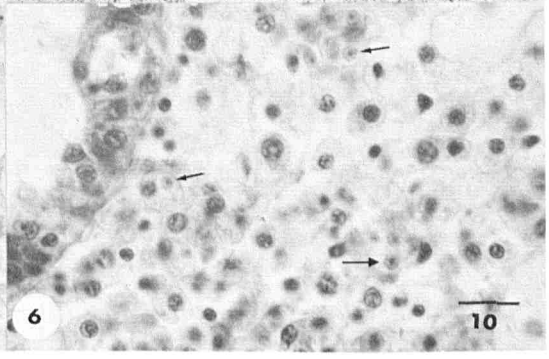
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TABLE 2.—Percentage of prevalance of lesions and parasites in Denman Island oysters.

Code	Date	Granulocyte infiltration (%)	Tissue abscess (%)	Hyaline hemocyte infiltration (%)	Neoplasms (%)	Microcell infection (%)	Mytilicola (%)	Ciliates	
								Gill (%)	Other (%)
WWC-1	22 May 1967	33	7	0	0	7	7	4	4
WWC-2	5 June1967	4	18	0	0	14	4	4	0
WWC-3	10 Apr. 1968	40	16	0	0	4	0	0	0
WWC-4	22 Apr. 1968	0	16	0	0	16	0	0	4
WWC-4	24 May 1968	8	4	0	0	4	0	0	4
WWC-6	24 June1968	32	4	24	0	0	0	0	0
WWC-7	5 Aug. 1968	0	0	0	0	0	0	0	0
WWC-8	14 Oct. 1968	36	0	0	4	0	0	0	0
WWC-9	18 Nov. 1968	12	7	36	8	0	0	0	0
WWC-10	27 Jan. 1979	20	0	8	0	0	0	0	0
WWC-11	26 Feb. 1969	4	0	0	0	0	0	0	0
WWC-12	21 Mar. 1969	8	4	0	0	4	8	0	0
WWC-13	11 Apr. 1969	20	20	8	0	12	0	4	4
WWC-14	12 May 1969	24	32	0	8	16	0	0	0
WWC-15	30 June1969	8	12	0	0	0	0	0	0
WWC-18	9 June1980	4	20	0	0	16	8	0	0

systemic with diffuse inflammatory infiltration of connective tissue (Fig. 5) associated with the presence of microcell parasites (Fig. 6). Microcells were cytozoic in hemocytes and VCT. Focal abscesses were present but not nearly as prominent in the Hawaiian oysters as the lesions in Denman Island oysters.

Australian Winter Disease Studies in *Saccostrea commercialis*

Australian winter disease was characterized by pustules, ulcerations, and abscesses (Fig. 7). Seven individuals, consisting of six females and one male, displayed ulcerations in the gonad and mantle. Ulcerations of the gills were also common and frequently occurred near the adductor muscle. Impaired adductor muscle contraction was characteristic of the disease.

Histologically, the animals contained abscesses (Fig. 8) with intense phagocytic infiltrations in the connective tissue and varying degrees of necrosis. The abscesses contained a small (1–2 μm) organism (Figs. 9, 10) which contained a nucleus >1 μm that was spherical with bipolar or eccentric nucleolar structures. The size and cytozoic location of these organisms suggest a strong similarity to other microcell type parasites seen in other species of oysters. Four of the six females had gonads in a state of resorption and digestive diverticular epithelium was slightly metaplastic in two of the seven oysters.

Microcell Disease Study in *Ostrea edulis*

Episode 1

Microcell disease in *O. edulis* from progeny from Boothbay Harbor, ME brood stock spawned at Milford, CT and transferred to Chincoteague Bay, MD (Code FK).

Two of the 13 oysters fixed between August 1961 and July 1962 had heavy infection of microcells (Fig. 13) which were 1–3 μm in diameter with a Feulgen-positive nucleus (1 μm diameter) and found intracellularly within hemocytes. In three of the other oysters, moderate infiltrations of hemocytes were observed but without parasites.

FIGURE 1.—Right and left valves of *Crassostrea gigas* from Denman Island, British Columbia. The darker rounded lesions are conchiolinous shell pustules characteristic of the Denman Island disease.

FIGURE 2.—Scale units in Figures 2–15 are in micrometers. Macrophotograph showing shell pustule (A) and adjacent tissue ulcer (B).

FIGURE 3.—Histologic section from Denman Island oyster. A large abscess-type lesion is apparent in the connective tissue-gonad region of the section. 100×. Feulgen picromethyl blue (FPM) stain (specimen WWC-2-7).

FIGURE 4.—Higher magnification photomicrograph taken at the edge of the lesion in Figure 3. Many microcell protistan parasites (*Mikrocytos mackini* sp. n.) are evident in vesicular connective tissue cells adjacent to necrotic inflammatory cells deeper in the lesion. 1,000×. Harris' hematoxylin and eosin (HHE) stain (specimen WWC-2-7).

FIGURE 5.—Lesion caused by microcell infection in *C. gigas* from Hawaii. 100×. HHE stain (specimen S-124A-45).

FIGURE 6.—High magnification photomicrograph showing microcell parasites intracellular in hemocytes in vesicular connective tissue of the Hawaiian oyster. 1,000×. HHE stain (specimen S-124A-45).

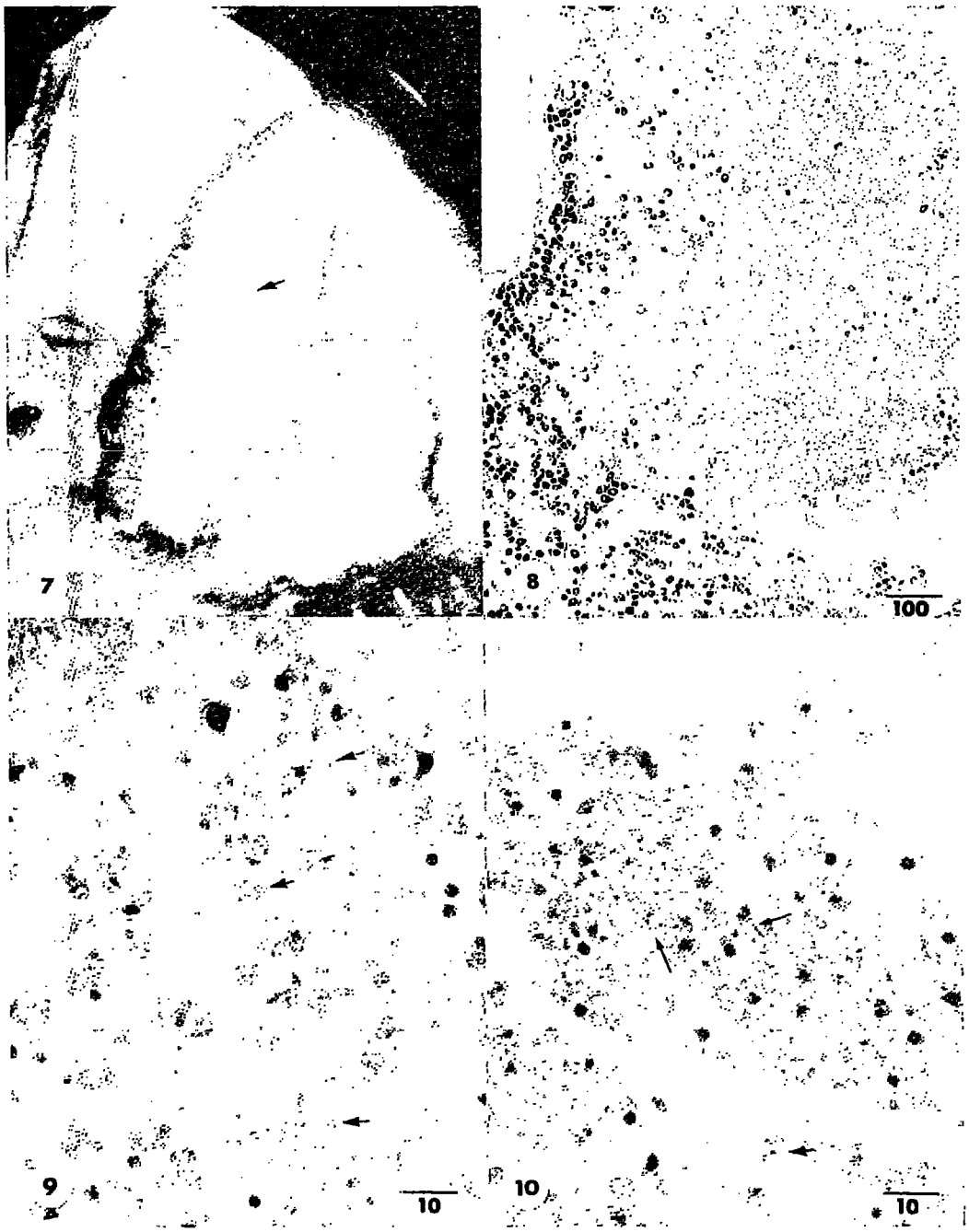


FIGURE 7.—Ulceration in the mantle of *Saccostrea commercialis* with Australian winter disease.

FIGURE 8.—Large abscess-type lesion in the connective tissue-gonad region of *Saccostrea commercialis* (code S-41-7) from Australia with Australian winter disease. 100×. HHE stain (specimen S-41-7).

FIGURE 9.—Higher magnification photomicrograph from lesion in Figure 8. Note intracellular microcell parasites (*Mikrocytos roughleyi* sp. n.) with hemocytes. 1,000×. HHE stain (specimen S-41-7).

FIGURE 10.—Heavy infection of Australian winter disease; microcell parasites in the gonad of S-41-4. 1,000×. HHE stain.

Episode 2

Microcell disease in *O. edulis* transferred from Milford, CT to Elkhorn Slough, CA (Code WAC).

Epizootiological gross and histopathologic data are presented in Table 3. Clear association is apparent between high mortality, emaciation (watery condition), mantle recession, hemocytic infiltration, and heavy microcell infection.

Infections were particularly intense in gill and GI tract epithelia which contained dense infiltrations of infected hemocytes (Fig. 11). Infections were characterized by the intracellular (in hemocytes) and extracellular presence of "microcell" organisms (Fig. 12) similar to those seen in the Chincoteague Bay (FK) samples.

Episode 3

Microcell disease in *O. edulis* transferred from Milford, CT to aquaria in Oxford, MD (Code FMT).

The experiment ran from 20 February 1968 until 9 October 1968. No transmission was noted. However, tank C drained accidentally on 19 March and the filtered seawater was replaced with unfiltered seawater from Chincoteague Bay, VA. A combined total of 9 of 11 animals died between 22 March and 27 March and the remaining 2 live oysters were fixed on 28 March.

The first six that died were from tank C and had moderate to heavy cases of microcell disease with associated hemocytic infiltration. Histologic examination of both species, either after mortalities, or when they were sacrificed in October, failed to reveal any more infections. The parasites and disease characteristics were identical to the previously described cases (Fig. 14).

Microcell Disease Study in *Ostrea lurida*

Microcell disease in *O. lurida* from Yaquina Bay, OR (Codes WAO-7-A and WAO-12-A).

Monthly to bimonthly samples of 50 specimens were examined grossly and for histopathology for a 2-yr period. A 24% prevalence of microcell disease was seen in WAO-7-A samples collected in February 1969, and 12% prevalence was seen in the WAO-12-A samples collected in February 1970. No microcell infections were seen in any of the other samples. However, neoplasms and *Mytilicola orientalis* infections were seen commonly throughout the study.

Microcell infections tended to be less intense than in *O. edulis*, but organisms were similar in size and appearance to the organisms seen in flat oysters (Fig. 15). Intracellular infections were in VCT cells and not hemocytes.

Ultrastructural Studies

Electron microscopy revealed *O. edulis* parasites that were usually intracellular with up to three organisms per cell. Parasites were 1–3 μm in diameter, and contained an eukaryotic nucleus about 1 μm in diameter. A crescent-shaped, peripheral nucleolus was evident in most organisms (Fig. 16). The cytoplasm contained numerous ribosome-like organelles and spherical dense bodies, presumably membrane bound, which were 90–130 nm in diameter, and generally resembled the "haplosporosomes" (Fig. 17) described in other haplosporidan

TABLE 3.—Epizootiology of microcell disease in *O. edulis* from California.

Code	Stock origin	Sample location	Date fixed	Mortality	*N*	Condition			Mantle recession	Hemocyte infiltration	Microcell infection
						Fat	Med	Watery			
WAC-1 (1–20)	Milford 1964	Morro Bay	7 Dec. 1965	Heavy	20	no gross data				18	18
WAC-2 (1–25)	Milford 1964	Pigeon Pt.	1 May 1966	Heavy	38	1	8	19	22	25	25
WAC-3 (1–10)	Milford 1964	Morro Bay	1 May 1966	Heavy	10	2	6	2	6	8	8
WAC-3 (11–15)	Milford 1963	Morro Bay	1 May 1966	Low	5	4	1	0	0	0	0
WAC-3 (16–26)	Milford 1963	Morro Bay	1 May 1966	40%	10	6	4	0	1	6	3
WAC-3 (27–31)	Milford 1965	Morro Bay	1 May 1966	0	5	5	0	0	0	0	0
WAC-4 (1–5)	Milford 1964	Tomales Bay	1 May 1966	Low	5	5	0	0	1	0	0

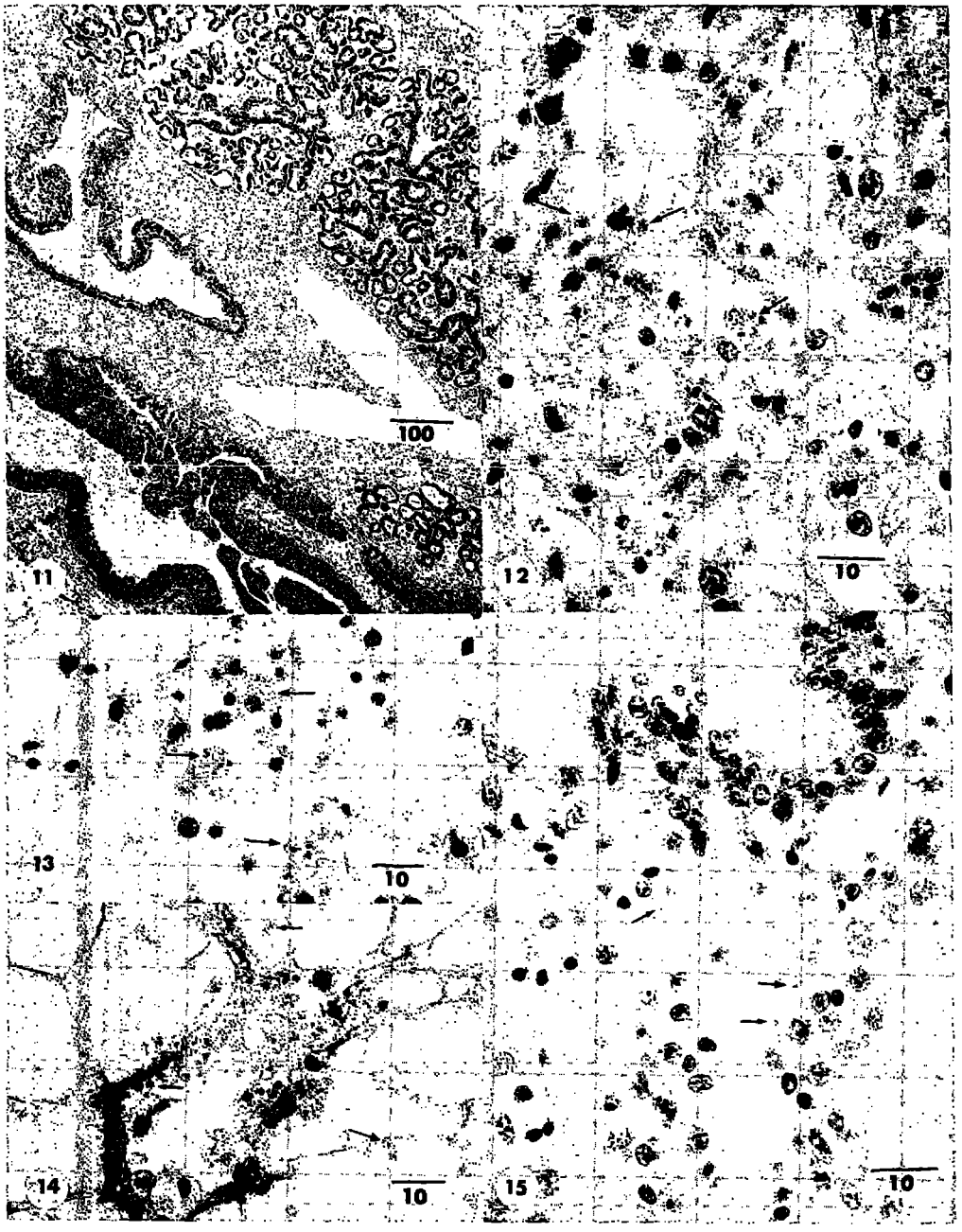


FIGURE 11.—Low magnification view of *Ostrea edulis* from California (WAC-2-29). Note diffuse inflammatory infiltrate in vesicular connective tissue. 100×. HHE stain.

FIGURE 12.—Microcell infection in *Ostrea edulis* (specimen WAC-2-19) from population of oysters introduced into California waters from Milford, CT. 1,000×. HHE stain.

FIGURE 13.—Microcell infection in hemocytes in *Ostrea edulis* transported from Milford, CT to Chincoteague Bay, VA in 1962 (first diagnosed case of *Bonamia ostreae*). 1,000×. HHE stain (specimen FK-5-1).

FIGURE 14.—Microcell infection in *Ostrea edulis*. Transferred from Milford, CT to Oxford, MD recirculated seawater aquarium. Cells of the vesicular connective tissue are infected. 100×. HHE stain (specimen FMT-B-1-3).

FIGURE 15.—Microcell infection in vesicular connective tissue and hemocytes of *Ostrea lurida* from Yaquina Bay, OR. 1,000×. FPM stain (specimen WAO-7A-41).

parasites (Perkins 1979). Larger "membrane" bound structures (500 nm) consistent with the appearance of mitochondria were also present in the cytoplasm; however, cristi could not be distinguished.

Ultrastructural studies were also performed on positively diagnosed oysters (*C. gigas*) from Denman Island, British Columbia (sample WWC-18, collected 9 June 1980). Microcells were always associated with focal abscesses, but their occurrence was restricted to the periphery. Parasites were found as cytozoic organisms primarily in VCT cells (Fig. 18). Microcells were 3–4 μm in diameter, had nuclei 1 μm in diameter, and nucleoli 250–300 nm in diameter. Nucleoli were spherical, eccentrically located within the nucleus, but never peripheral (Fig. 19). One to many parasites occurred within the cytoplasm of vesicular cells. None were ever found within hemocytes. Figure 20 shows an organism possibly undergoing division. The cytoplasm was densely packed with free ribosomes and contained a variety of organelles as follows: double membrane bound dense bodies 50–185 nm in diameter (Fig. 19A); double membrane bound, dumbbell-shaped structures (Figs. 20, 21h), approximately 37 × 18 nm to 85 × 260 nm; and dense bodies 40–45 nm in diameter that appeared to be membrane bound, and a suggestion of six- and five-side angularity (Figs. 19, 20, 21v). Endoplasmic reticulum was extremely sparse if present at all. The plasma membrane complex consisted of possibly two membranes with the external membrane containing dense material. An electron-lucent zone was present around the cell, suggestive of a glycocalyx.

Taxonomic Descriptions

The information acquired on these diseases and the organisms associated with them and outlined previously allows us to propose taxonomic descriptions of them.

Mikrocytos g. n. (*Protista incerta sedis*) (little cell) — Definitive life cycle stages that would permit higher classification of this protistan parasite have not been observed. Named after the term microcell as coined by the late John G. Mackin. Small (1–4 μm), unicellular, protistan, cytozoic parasite normally infecting VCT cells of oysters. Always associated with abscess-type focal inflammatory lesions.

Type species - *Mikrocytos mackini* sp. n.

Bonamia, the other closely similar genus, infects hemocytes of ostreid oysters only and is associated with systemic non-abscess type disease manifestations.

Mikrocytos mackini sp. n. — Named in honor of the late John G. Mackin who discovered this parasite in the early 1960s.

Type specimen - A 6 μm thick hematoxylin-and-eosin-stained histologic section of an infected oyster, *C. gigas* (WWC-2-7), was deposited in the Registry of Marine Pathology, Northeast Fisheries Center, Oxford, MD 21654.

Host - *Crassostrea gigas*

Type locale - Henry Bay, Denman Island, British Columbia, Canada.

Range - Occurrence confined to above site. (A closely related candidate for inclusion within this species was found in *C. gigas* from Hawaii.)

Morphologic characteristics - Small, 1–4 μm intracellular parasites of VCT cells; infections always associated with focal inflammatory tissue abscesses. Parasites are unicellular and contain a small 1 μm nucleus that has an eccentric nucleolus 250–300 nm in diameter. The cytoplasm contains dense, double membrane bound, dumbbell-shaped haplosporosome-type organelles 50–180 nm in diameter and 40–45 nm membrane bound five- and/or six-sided dense bodies.

Mikrocytos roughleyi sp. n. — Named in honor of T. C. Roughley who published the initial study of the Australian winter disease in the 1920s.

Type specimen - A 6 μm thick hematoxylin-and-eosin-stained section of an infected oyster, *S. commercialis* (S-41-7), was deposited in the Registry of Marine Pathology, Northeast Fisheries Center, Oxford, MD 21654.

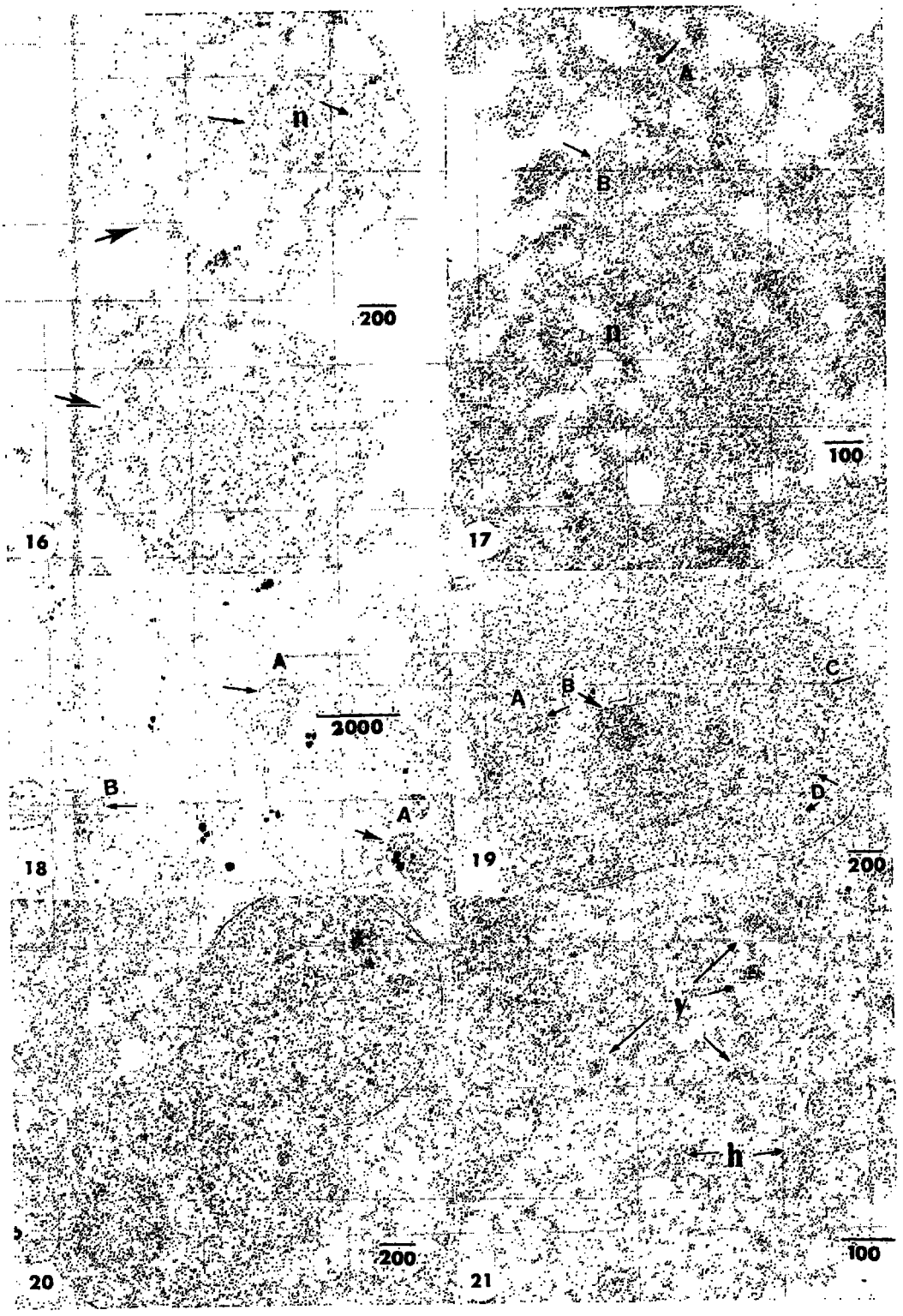
Host - *Saccostrea commercialis*

Type locale - Georges River, Woolooware Bay, New South Wales, Australia.

Range - Known only from the above location and other high salinity estuaries in this region of New South Wales.

Morphologic characteristics - Infections occur in hemocytes and are associated with focal abscess-type lesions in the gill, connective, and gonadal tissues. Organisms are small 1–3 μm cells that contain an eccentric nucleus and a cytoplasmic vacuole. Ultrastructural characteristics are not known.

Comparisons — *Mikrocytos* g. n. is always associated with focal abscesses and occurs in crassostreid oysters. *Bonamia* is always associated with generalized infections and only occurs in ostreid oysters.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Mikrocytos mackini sp. n., which has eccentric nucleoli, and *M. roughleyi* sp. n., which has a cytoplasmic vacuole and a nucleus that is displaced to the periphery of the cell, are morphologically distinct from *B. ostreae* (the only closely related species). All three species occur in separate host species and all appear to be host specific.

DISCUSSION

Denman Island Disease

Quayle's original study (1961) documented heavy mortality (40%) clearly associated with surface tissue pustules in *C. gigas* in an area of British Columbia in May. Studies of *C. gigas* by Mackin resulted in the discovery of the "microcell" organism and its association with tissue abscesses. Subsequent histological examinations done by the senior author, in cooperation with D. Quayle and N. Bourne, confirmed the association of mortality, pustules, tissue abscesses, and microcell infections that have continued to occur during each May and June to the present time.

Histopathologically, this disease (caused by *Mikrocytos mackini*) is characterized by acute inflammatory abscesses which remain focal until the oyster dies or resolution occurs. While microcell organisms are not always found in abscesses, they are never found in oysters that do not have abscesses, indicating at least an associational relationship.

Electron microscopy has demonstrated only one stage of a small protistan organism that contains organelles resembling haplosporosomes. No clear demonstration of mitochondria has been accomplished. The haplosporosome-like organelles often tend to be elongated and contain layers of membranes. Internal structure of these organelles is not nearly as dense as that seen in *Bonamia* or other haplosporidans.

The small 45 nm dense bodies also seen in the cytoplasm have characteristics suggestive of virus structure; namely, uniform size, abundant occurrence in the cytoplasm only, and a suggestion of icosahedral symmetry. The cytoplasmic occurrence, 46 nm size, icosahedral symmetry, and the presence of an envelope are characteristics of the family Togaviridae. The lack of paracrystalline arrays, strategy of development, empty capsids, and extracellular occurrence prevent conclusive identification of these particles as virus at this time, and these may prove to be an exclusive organelle that is a characteristic of this protistan group. The presence of a lytic virus in the parasite could also explain the self-limiting nature of the focal abscesses characteristic of the Denman Island disease.

Australian Winter Disease

Since Roughley described this disease in an Australian *S. commercialis* in 1926, little progress has been made toward identification of the etiologic agent. Careful examination of the tissues of affected animals, collected by Peter Wolf, has revealed apparent small cytologic and histozoic organisms associated with abscesses. These organisms have features such as size, morphology, and tissue location remarkably similar to organisms present in other oyster microcell diseases. Peter Wolf (unpubl. data) has stated that this disease thrives in high (30–35‰) salinity (and is unknown in lower salinities); the incubation period is about 2½ months and mortality does not occur in animals less than 3 years old. The occurrence of shell lesions and focal tissue abscesses appears to be common features in *Saccostrea* and *Crassostrea*. This may indicate a degree of resistance characterized by the ability of the animal to isolate parasites in a focal lesion and to eliminate them by either rupture of the abscesses or diapedesis through the mantle epithelium to the shell surface, with subsequent calcification via shell pustule formation, or it may indicate a host parasite relationship response. This mechanism was reported in oysters that had acquired resistance to *Haplosporidium nelsoni* (Farley 1968).

Kern (fn. 6) found microcell infections in *C. gigas* from Hawaii (Fig. 6) that were not always associated with focal abscesses. General systemic infection and inflammatory infiltration were noted in these cases (Fig. 5), but the organisms appear

FIGURE 16.—Scale units in Figures 16–21 are in nanometers. Electron micrograph of deparaffinized *Ostrea edulis* from California. Two intracellular microcells showing prominent nuclei with peripheral nucleoli. 36,000×.

FIGURE 17.—Higher magnification of California microcells showing haplosporosome-like bodies (A) and a probable mitochondria (B). 108,000×.

FIGURE 18.—Electron micrograph of several microcells in vesicular connective tissue of *Crassostrea gigas* (A) from Denman Island, British Columbia. Probable degenerate microcells can also be seen in the cytoplasm of phagocytic hemocytes (B). 7,320×.

FIGURE 19.—Electron "micrograph" of microcell from Denman Island *Crassostrea gigas*. Note the eccentric nucleolus (A), myelin bodies (B), haplosporosome-like bodies (C), and virus-like entities (D). 36,900×.

FIGURE 20.—Electron micrograph of *Crassostrea gigas* microcell with structure suggestive of division. 36,900×.

FIGURE 21.—Higher magnification of electron micrograph showing haplosporosomes and virus-like dense bodies. 108,000×.

to be identical to the Denman Island microcell organisms.

Microcell Infections in *Ostrea edulis*

Microcell infections were first seen in *O. edulis* in moribund oysters which had been transferred from Milford, CT to Chincoteague Bay, VA in 1962. Two animals from the FK sample had developed clinical manifestations of the disease. Other cases appeared in animals transferred from Milford to California, and Milford to Oxford. Morphology of the infectious organisms was identical in all of these episodes and the histopathology always consisted of acute inflammatory infiltration and systemic involvement. All episodes were associated with movement of oyster stocks originating in Milford, and all experienced severe mortality. No differences were noted between any of the *O. edulis* epizootics in regard to morphology of the organisms. Comparison of the American *O. edulis* infections with tissues of French oysters experiencing *B. ostreae* infections (Pichot et al. 1979; Balouet et al. 1983) revealed no morphologic or histologic differences at the light or electron microscope level. Indeed, ultrastructural comparisons demonstrate close similarities. Size comparisons of organisms are identical and the nucleus contains a peripheral nucleolus, and identical haplosporosome-like organelles are present in the cytoplasm. The major difference is in epizootic occurrences. The French epizootic occurred in natural or feral populations of European flat oysters. Since introduction of oysters to French sites from locations outside of France was a common event in the past, the source of the index case may have originated from an introduction of oysters from Elkhorn Slough, CA in the late 1970s (Elston et al. 1986). Contagious spread (Tige et al. 1981) is well documented in many locations in France and also the Netherlands. With the exception of the established breeding populations of flat oysters in the central Maine coast region, no natural or feral populations of *O. edulis* exist in the United States. The State of Maine carefully controls imports into the state; the disease has not been established in this population. The discovery of microcell infections in *O. lurida* in Oregon suggests that this may be a naturally occurring disease in that species. Infection intensity and prevalences suggest that some animals may die from the disease. The disease appears to be enzootic in the Oregon location. The lack of ultrastructural studies prevents close comparison of the *O. lurida* disease with the *O. edulis* disease. However, the disease in *O. lurida* tended to infect VCT while *B. ostreae* is primarily a disease of hemocytes.

CONCLUSIONS

There is a complex of oyster diseases caused by a group of protistan parasites of several species. These small intracellular and extracellular organisms designated originally as microcells have been found in association with serious disease in two species of *Crassostrea* and two species of *Ostrea*. It appears that the disease in *C. gigas* and *S. commercialis*, while exhibiting some similarities in types of lesions, are probably caused by different species of microcell type parasites.

A new genus, *Mikrocytos* g. n., and two new species have been described for the organisms causing disease in oysters: *Mikrocytos mackini* sp. n. in *C. gigas* from British Columbia, Canada, and *Mikrocytos roughleyi* sp. n. in *S. commercialis* from Australia.

Disease that has struck *O. edulis* in France is identical to the microcell disease seen in *O. edulis* in three episodes in the United States. The organism causing the disease in *O. edulis* is *Bonamia ostreae* and is clearly different from the microcell organism found in *C. gigas* in British Columbia and Hawaii. Finally, additional ultrastructural studies are needed for more complete characterization of the organisms from *O. lurida* and *S. commercialis*.

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NOTES

CONJOINED TWIN ADULT SHRIMP (DECAPODA: PENAEIDAE)

A two-headed roughback shrimp, *Trachypenaeus similis* (Smith), caught at the entrance to Galveston Bay, TX 10 May 1987 by Harold Fraley, together with a color photograph of the specimen taken subsequent to capture, was sent to me for identification, morphological examination, and deposit in the crustacean collection of the National Museum of Natural History (USNM 234419), Smithsonian Institution.

The specimen (Fig. 1) is composed of two cephalothoraxes (heads) perfectly aligned with the median sagittal plane and conjoined posteriorly to an unpaired, normally segmented abdomen. The cephalothoraxes and abdomen were disarticulated when the preserved specimen reached me in October 1987, but were restored to normal position easily with aid of the photograph as a guide. The lower cephalothorax is that of an adult female, carapace length including rostrum 32 mm, short carapace length (orbital margin to posteromedian edge of carapace) 21 mm; respective measurements for the upper carapace are 34.4 mm and 21.7 mm. The abdomen is flexed and twisted to the left, and the fourth and fifth segments are damaged, hence its length cannot be measured accurately. Comparison of the specimen with spermatophore bearing females of the species in the USNM crustacean collection indicates that it is adult in size, about 85 mm total length.

Shrimps are sometimes caught and preserved while in the act of molting. In that event the carapace being molted tends to be loosened at the thoraco-abdominal juncture so that its posterior end can be flipped dorsally and away, freeing the husk-like old carapace from the underlying soft new carapace. A first impression that this specimen was caught and preserved while in the act of molting was not borne out by the structures observed.

The integument of each carapace is firm, as is that of the other exoskeletal parts. Both carapaces are similar in shape and structure, including the part of the lower carapace that is hidden by the upper one. It is noteworthy that the upper carapace is larger than the lower, just the opposite of what would be expected if the upper one represented an ecdysial discard. Eyes in both heads have normal dark corneal pigment, though the corneal surfaces are shriveled by preservation. Antennules, anten-

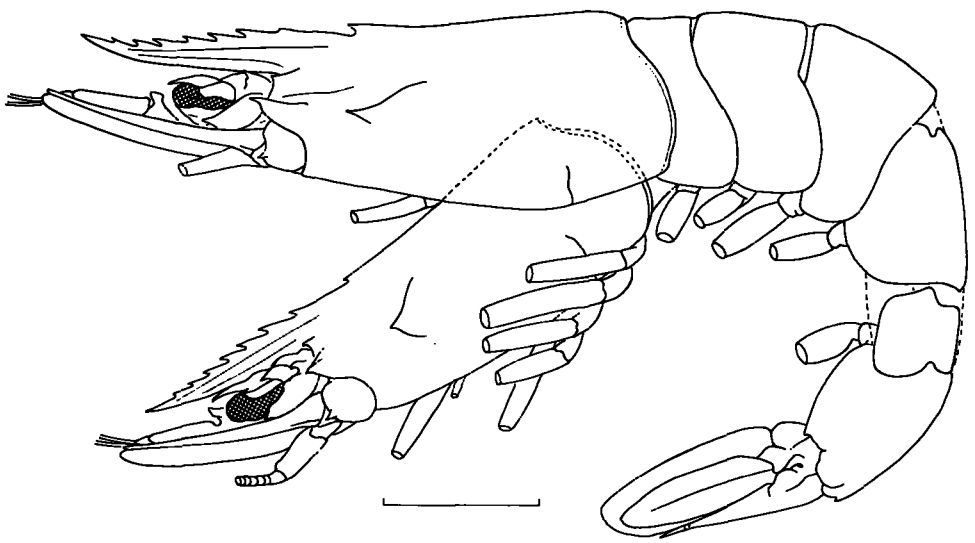

FIGURE 1.—Conjoined twin *Trachypenaeus similis* in diagrammatic lateral view, distal parts of appendages intentionally deleted, except for those of uropods. Scale = 1 cm.

nae, mandibles and associated palps, first and second maxillae, and first, second, and third maxillipeds are present and apparently normal on both heads, though the antennal flagella are broken and the right third maxilliped has apparently been lost from the upper head. Similarity in the cephalothoraxes is limited to features pointed out above.

The lower cephalothorax has normal appendages and internal organs, or traces of them, except for some broken and missing articles on the pereopods. The heart, hepatopancreas, and gonads apparently disintegrated during the interval of time between capture and fixation, hence lost all traces of their conformation in life. Fluids from the disrupted circulatory system were fixed as irregular clots. The mouth, esophagus, stomach, and a fragment of the gut are present, though the latter is connected neither to the pyloric stomach nor to the sector of intestine that courses through the abdomen to the anus. However, one can visualize that the path of the intestine in the lower cephalothorax was functionally normal before it was disrupted by breakdown of the other internal organs that surrounded it in life.

The upper cephalothorax lacks a mouth, the sternal plate between the mouthparts is not perforated, and there is no esophagus, stomach, or fragment of intestine. It seems therefore that the upper cephalothorax, though equipped with normal head appendages, could not function in feeding. Moreover, the rear part of the upper cephalothorax fitted over the rear part of the lower one like a firmly pulled down cap, with its branchiostegites deeply overlapping those of the lower one. In this arrangement the posterior part of the lower cephalothorax filled the space that would normally have been occupied by pereopods, external reproductive structures, thoracic endophragmal system and body wall, gills, and internal organs of the upper cephalothorax. As a result there was little or no room for development of these structures in the upper cephalothorax, although there may have been a heart. The membrane that lined the branchiostegites and body wall of the upper cephalothorax seems to have extended backward from the region of the cervical groove to merge with its counterpart in the posterior region of the lower cephalothorax, and with the normal integumental lining of the abdomen in order to have maintained confluence in the blood sinuses.

The abdomen, though crushed at the level of the fourth and fifth segments, bears normal pleopods, uropods, and telson. The anterior end of the abdominal muscle mass is preserved in a shape that fits the posterior end of both cephalothoraxes, but the main connection extended into the functional lower one in which complete organ systems were located.

There is a large literature treating malformations of decapod crustaceans, primarily lobsters, freshwater crayfishes, and crabs, but there is little published information of this sort on shrimps (Bateson 1894; Johnson 1968; Johnson and Chapman 1969; Pauley 1974), aside from the subject of disease which is not at issue here (Couch 1978). The most exhaustive account is that of Bateson who, along with many others before and after, discussed duplication of parts, intersexes, and malformations that occur during molting, Pérez Farfante (1980), for example, noted anomalous intersexes in the Indo-West Pacific needle shrimp, *Penaeopsis rectacuta* (Bate). The majority of these accounts treat malformed limbs or their parts (for a well-illustrated example see Shuster et al. 1963). Fewer studies are concerned with teratology.

Monsters with fused double cephalothoraxes, though rare, have long been known among larvae of the lobsters *Homarus americanus* H. Milne Edwards and *H. gammarus* (Linnaeus) (Herrick 1896, 1911). Ryder (1886) noted four forms of conjoined twins in larval American lobsters: lateral fusion of cephalothoraxes that demonstrated absence of eyes, possession of a single median eye or paired eyes representing the right eye of the right larva and left eye of the left larva, while the abdomens of each type were separate and divergent at a wide angle, and cephalothoraxes of two embryos fused together along their dorsal surfaces, with full complement of eyes, appendages, and separate abdomens, but with internal organ systems fused. Ryder attributed all of these twinnings to fusion coincident with the process of gastrulation and gradual formation of the embryos. Herrick (1896, 1911) discussed and figured some of these cases also but thought that fusion came later in development than gastrulation.

I have found no account of conjoined twinning in shrimps, and no report of twinning that parallels the case presented here. What is amazing is that an animal so bizarre could molt at all, let alone progress through a series of molts to attain mature size. Whether the deformity resulted from embryonic malformation or from subsequent injury cannot now be determined, although angle of divergence and median sagittal alignment of the cephalothoraxes suggests that the malformation resulted from aberrant molting.

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NOTE ON MUSCLE GLYCOGEN AS AN INDICATOR OF SPAWNING POTENTIAL IN THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*

During the reproductive cycle of the Atlantic sea scallop, *Placopecten magellanicus*, glycogen levels rise and fall in the hemolymph (Thompson 1977) and in the adductor muscle (Robinson et al. 1981; Gould 1983), reflecting the buildup of glycogen reserves in the muscle and their later transfer to the gonad. Muscle glycogen normally rises to a yearly peak in spring after the phytoplankton blooms, then is transferred to the gonad for gamete differentiation and maturation (Robinson et al. 1981). The glycogen transfer is followed by an increase in size of the maturing gonad and a loss of muscle weight (Gould 1983). During the autumnal algal blooms, glycogen levels in the muscle rise again slightly and drop thereafter to an annual low during the winter months, when the small energy reserves are used for basal maintenance and to initiate gametogenesis.

Glycogen reserves from the muscle and lipid reserves from the digestive gland are the major sources of stored energy supplied to the scallop gonad. High spring glycogen levels most dramatically indicate the degree of buildup of energy stores used to fuel gamete differentiation and maturation, whereas low winter muscle glycogen levels correspond to the postspawning exhaustion of reserves. Winter values higher than the normal range for any given population, therefore, could indicate an unusually large and extended period of nutrient availability, but more probably would suggest resorption of gametes.

We suggest, therefore, that the spring peak and the winter ebb of muscle glycogen be used as measures of the relative spawning potential and spawning success, respectively, for *Placopecten*. Sampling during these two seasons may readily provide information on the recruitment contribution of different scallop populations.

Timing of the seasonal high and low values for this metabolic parameter can vary by several weeks from year to year, reflecting the timing and intensity of phytoplankton blooms (themselves dependent on other environmental variables), and the time and degree of success in spawning. To obtain a practical data base for this major measure of seasonal energy reserves, therefore, we sampled a single bed of sea scallops off Asbury Park, NJ, on a year-round monthly basis for 3½ years. In examining mean annual high and low muscle glycogen values for these scallops, data were averaged for animal collections

from mid-April through June each year to arrive at a general value for the spring buildup and peak. Although such values do not indicate the maximal glycogen values, which may be reached either gradually or quickly in any of those months, an average better enables year-to-year comparisons. Data for collections from late November through February were similarly averaged to obtain a value for the postspawning winter period of low muscle glycogen.

We used this same parameter for specimens collected from random sites in the Gulf of Maine, and found a different seasonal pattern in scallops from depths greater than ca. 110 m. Because these deepwater sea scallops came from many different sites in the Gulf of Maine, data were averaged for each collection date for each site. This report presents our data for spring and winter adductor muscle glycogen in a single subtital sea scallop population for the years 1981–84, and in deepwater sea scallops from the Gulf of Maine for 1980–82.

Materials and Methods

Asbury Park sea scallops were collected by trawl from a site 31 m deep on the southern shelf of the Hudson River Canyon off Asbury Park, approximately 37 km NNE of Manasquan Inlet (ca. 40°13′ × 73°47′). Collections were made at monthly intervals from spring 1981 through late July 1984 and during two intensive weekly sampling periods from early May through mid-June in 1983 and 1984, to monitor the spring buildup of muscle glycogen. For some months, particularly in the spring of 1982, collections were not available. Each collection comprised 6 males and 6 females (shell height 95–110 mm). The sea scallops were held overnight in 5°C aerated seawater at the Northeast Fisheries Center's (NEFC) laboratory at Sandy Hook, NJ, and transported the following day in a cooler to the Milford, CT, NEFC laboratory. For transport, the sea scallops were placed on top of paper toweling that had been soaked in seawater, then wrung out and layered over ice enclosed in a sealed plastic bag. The animals were dissected the same day, and all tissue specimens were stored at −80°C until testing. Gonad volumes were also noted. Deepwater sea scallops were dissected on shipboard immediately after collection by trawl, and the muscle tissue held at −40°C while at sea, then transferred on dry ice to the −80°C freezer in Milford. Because we relied on volunteer help for many of these collections, gonad data were not always available for shipboard samples of adductor muscle from deepwater sea scallops.

Muscle dissection, tissue preparation, and the procedure for glycogen analysis are described in detail elsewhere (Gould et al. 1985); glycogen levels are presented as μg of glucose per gram of wet tissue (μg g^{-1}). Because there were no detectable differences between sexes for muscle glycogen levels, data for males and females were combined.

Results and Discussion

Asbury Park Sea Scallops

In the spring of 1981, the Asbury Park sea scallops had muscle glycogen levels averaging higher than 2,000 μg g^{-1} (Table 1). Such levels are not uncommon in well-fed scallop populations, as observed during several years of monitoring activity on the continental shelf off New England and the mid-Atlantic states (Gould 1981, 1983) during the NEFC's Ocean Pulse/Northeast Monitoring Program (NEMP) and the NEFC's Resource Assessment surveys. The mean annual low levels in the

TABLE 1.—Seasonal high and low levels in adductor muscle glycogen for both males and females in a single population of sea scallops off Asbury Park, NJ. Values were averaged for mean seasonal highs during and after spring phytoplankton blooms (April, May, June) and for mean seasonal lows after spawning (December, January, February). Gonad volumes are also shown for the same time periods.

Year	Season	Sample N	Muscle glycogen (μg g^{-1}) $\bar{x}$	Muscle glycogen (μg g^{-1}) SE	Annual ratio spring:winter	Gonad volume (mL) $\bar{x}$	Gonad volume (mL) SE
1981	Spring	34	2,217	283		no data	
1982	Spring	24	544	32		5.42	0.74
1983	Spring	84	610	15		6.23	0.29
1984	Spring	72	254	12		4.51	0.24
1981–82	Winter	22	203	18	10.9	6.50	0.47
1982–83	Winter	24	226	14	2.4	3.00	0.46
1983–84	Winter	12	490	57	1.2	2.75	0.39

Asbury Park sea scallops the following winter were within the normal range (200–300 $\mu g\ g^{-1}$) observed for sea scallop populations over those same years of monitoring.

In 1982 and 1983, the Asbury Park sea scallops were apparently adequately fed during the spring months, although glycogen levels were less than one third of those seen in 1981 and had no discernible peak. Muscle glycogen in the winter months of 1983 and 1984, however, was sufficiently high in both sexes (as compared with postspawning levels for this population, and with mean winter levels in other populations) to prompt the suspicion that gamete resorption had taken place, and that the 1983 spawning season had not been very successful. Moreover, although an intensive weekly sampling was performed in May and June 1984, we did not observe the normal seasonal increase in muscle glycogen; instead, the values resembled those of a typical winter low. When spring values for each year are compared with the subsequent winter's postspawning values (Table 1), a picture emerges of declining nutritional status from 1981 to the end of the study.

It is possible, of course, that the spring values in 1982 and 1983 were more typical for this population and that spring values for 1981 may have been unusually high. The latter phenomenon could have been the result of especially heavy phytoplankton blooms, or of oceanic currents favorable to the bottom settlement of planktonic nutrients. Certainly the most important single variable is nutrient availability.

The 1984 glycogen levels indicated either that little or no food was available to the sea scallops (at 30 m), or that they were not assimilating normally any food that was available. This phenomenon has yet to be explained satisfactorily, because the phytoplankton bloom in the area that year was extensive (J. O'Reilly[1]). Steven K. Cook[2] had suggested that some oceanographic event, such as the inshore intrusion of an offshore water mass known as the "cold pool" (e.g. Hopkins and Garfield 1979) may have caused an unusually early formation of a thermocline, one that effectively prevented settlement of planktonic detritus to the bottom. Whatever the reason, the Asbury Park sea scallops showed diminishing glycogen reserves for spawning from 1981 to the end of the study in 1984. Either planktonic nutrients were not reaching that population, or food was available but the sea scallops were not feeding or assimilating properly.

If the latter should be the case, it is perhaps relevant that the Asbury Park sea scallop population lies approximately 24 km downstream from the Christiaensen Basin, where general current patterns are southwesterly. Several active dumpsites are located in the Christiaensen Basin, including those for New York's sewage sludge and dredge spoils, where copper is a major contaminant (see Steimle et al. 1982). Moreover, as little as 10 $\mu g\ L^{-1}$ copper in the water column has been shown to interfere with gamete production and maturation (resorbing gametes) and probably also with feeding or nutrient assimilation in *Placopecten magellanicus* (Gould et al. 1985, 1988). Chemical analysis of tissues from these same Asbury Park sea scallops is under way, to determine whether metal levels were sufficiently elevated to induce this effect.

Deepwater Scallops

A data pattern for muscle glycogen similar to that seen in the Asbury Park sea scallops for 1984 has been observed in deepwater sea scallops taken from various sites in the Gulf of Maine (Table 2). These sea scallop beds were sampled randomly during the NEFC trawl survey cruises, and one fixed station was sampled seasonally during NEFC NEMP cruises (Gould 1981, 1983). Sea scallops taken from waters >110 m deep routinely showed very low glycogen levels throughout the year, the highest annual levels being reached in December. In the fall, vertical mixing of the subsurface and intermediate water increases to as deep as 150 m (McLellan et al. 1953; Colton 1968; Hopkins and Garfield 1979; Mountain and Jessen 1987), with the disappearance of any strong thermocline. In a recent comparison of food resources in shallow (20 m) and in deepwater (180 m) populations, Shumway et al. (1987) observed that a number of intact planktonic algal species reached the deepwater sea scallops after the fall phytoplankton bloom; this late annual food source "may provide just enough energy to sustain the population." On the whole, however, nutrient availability is very low at such depths, as indicated by the absence of chlorophyll in the deeper water column (J. O'Reilly[3]).

Deepwater sea scallops are visibly undernourished

[1]J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 428, Highlands, NJ 07732, pers. commun. October 1984.

[2]Steven K. Cook, National Weather Service, 2980 Pacific Highway, San Diego, CA 92101, pers. commun. March 1984.

[3]J. O'Reilly, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 428, Highland, NJ 07732, pers. commun. May 1985.

TABLE 2.—Mean seasonal high and low levels of adductor muscle glycogen in deepwater sea scallop populations of the Gulf of Maine.

Station coordinates		Date of collection	Depth (m)	Bottom temperature (°C)	Sample *N*	Mean gonad volume (mL)	Muscle glycogen ($\mu g\ g^{-1}$)
Lat.	Long.						
43°21′	[1]69°03′	01/29/82	160	7.0	12	2.25	153
43°23′	69°55′	04/23/80	168	4.2	5	—	303
43°25′	69°22′	04/23	180	4.9	5	—	164
43°16′	69°40′	04/23	159	4.0	5	—	248
43°20′	69°03′	05/07	155	5.0	5	—	282
43°21′	67°06′	05/07	155	5.0	4	—	274
42°49′	68°49′	05/10/81	202	6.0	2	—	145
43°07′	68°42′	05/10	174	5.5	8	—	199
43°30′	69°30′	05/24	144	4.2	12	—	178
43°33′	69°07′	05/24	152	8.4	4	—	180
44°21′	67°21′	08/03/82	137	10.4	12	4.70	178
42°56′	70°16′	08/16/80	155	4.9	8	—	226
43°26′	69°57′	08/16	134	5.3	9	—	120
43°21′	[1]69°03′	08/24/82	156	5.5 (at 100 m)	12	8.67	361
43°21′	[1]69°03′	09/07/80	155	6.0	18	9.09	133
43°17′	69°18′	11/04/80	161	6.0	10	—	437
43°18′	69°03′	11/04	167	7.2	10	—	330
43°00′	69°20′	11/04	181	5.8	10	—	318
43°37′	69°32′	11/04	113	8.1	5	—	582
43°21′	[1]69°03′	12/06/82	160	7.5	12	2.42	587
43°25′	69°22′	12/06	162	10.0	12	3.75	495
43°18′	70°03′	12/07	158	7.2	12	2.67	409
42°59′	70°10′	12/07	183	7.8	13	2.58	424

[1]Deepwater station off Toothaker Ridge that was sampled whenever possible; other stations were selected randomly during resource survey cruises.

(thin shells and small adductor muscles), lack the necessary glycogen reserves for successful spawning, and very probably resorb gametes. Moreover, bottom temperatures seldom reach 10°C (Mountain and Jessen 1987), the lowest temperature at which *Placopecten magellanicus* has been observed to spawn (Culliney 1974). In a recent study of a single deepwater sea scallop population in the Gulf of Maine, Barber et al. (1988) report reduced fecundity, followed by gamete resorption and a possible minor spring spawning, in turn followed by redevelopment, continued resorption, and an abrupt fall spawning attempt. Almost certainly, deepwater sea scallops do not spawn successfully. Recruitment to these beds, therefore, would be haphazard and originate both from populations on nearby ledges and from spatfall out of the Gulf of Maine gyre, from upstream spawning populations.

We have reported here that glycogen levels in *Placopecten magellanicus* adductor muscle, measured during the annual peak period in late spring and during the annual low period in winter, can indicate scallop populations with little energy reserves for successful spawning. In the case of the deepwater sea scallops in the Gulf of Maine, lack of available nutrients is undoubtedly the reason for their low muscle glycogen. Still to be clarified are the events leading to the 1984 failure of the Asbury Park sea scallops to develop the necessary energy reserves for spawning.

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VERTICAL DISTRIBUTION AND MASS MORTALITY OF PRAWNS, *PANDALUS PLATYCEROS*, IN SAANICH INLET, BRITISH COLUMBIA

Prawn, or spot prawn, *Pandalus platyceros* Brandt, 1851, British Columbia's largest shrimp species, is extensively fished in Canada and is of considerable economic importance (Noakes and Jamieson 1986). The species ranges from California to Alaska and, being largely associated with rocky terrain, is fished with traps in many of the region's coastal inlets (Butler 1980).

This study reports a fortuitous observation of catastrophic mortality of prawn in Saanich Inlet, noted during a series of observations on the vertical distribution of prawn on the walls of this fjord using a submersible. These observations are important because, under the circumstances involved, these mobile benthic organisms had ample opportunity to avoid the apparent rapid intrusion of lethal environmental conditions by moving upwards, and thereby remaining in a favorable environment.

Well-documented sudden mass deaths of adult marine invertebrates in subtidal environments have usually been associated with man-induced environmental perturbation, such as an oil spill, pollutant discharge, entrainment of organisms into a lethal environment (e.g., dredge or power plant cooling water intake), or the entrapment of benthic organisms by some lethal environmental event (Tulkki 1965). However, the selective high mortality of one or only a few species in a subtidal community, with no associated physical habitat perturbation and with apparent opportunity for escape, has been infrequently described in documented catastrophic mortalities (Brongersma-Sanders 1957; Swanson and Sindermann 1979; Levings 1980a, b; Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985; Renaud 1986). It is known that species differ in their relative tolerances to environmental stress (e.g., Renaud 1986), but for subtidal invertebrates, the proximity to lethal conditions of the majority of a population for extended time periods has not been generally noted. This study shows that prawn may occur close to lethal environmental conditions, and that abrupt mortality results if lethal water conditions suddenly intrude. In certain locations, such mortality may be more frequent than previously recognized and may justify a unique exploitation strategy.

Materials and Methods

This study was conducted between 6 and 10

October 1986, at Bamberton (lat. 48°35'N, long. 123°31'W), located half-way down Saanich Inlet, a 24 km long fjord on the southeast coast of Vancouver Island. Because of its close proximity to regional oceanographic laboratories, this inlet has been well studied oceanographically (Carter 1934; Herlinveaux 1962; Richards 1965; Anderson and Devol 1973; Pickard 1975; Emerson et al. 1979; Thomson 1981) and biologically (Tunnicliffe 1981; Burd and Brinkhurst 1984, 1985). At its mouth, it has a submerged (75 m) sill behind which there is a deep (maximum depth = 234 m) basin, and water below the sill depth is typically isolated, oxygen-deficient, and may contain hydrogen sulphide. The basin is flushed only when water above the sill is sufficiently dense to cascade into it. Throughout the year, there typically remains one or more oxyclines in the water column structure. The study area is generally characterized by a 20–30° slope to about 70 m, and a 30–60° slope from this depth to the bottom of the inlet (209 m).

Observations were made by two people from the submersible *Pisces IV*, which has been previously described by Mackie and Mills (1983). Two 3-h dives were made each day—one typically starting at 1300 and the other at 1900, about one hour after sunset. Dives to the bottom of the inlet were conducted at random locations over a 3 km length of shoreline and began with a direct descent to the bottom of the inlet. The submersible was then moved upwards, horizontal and about 1 m from the cliff, from the bottom of the inlet to a depth of 20 m. After surfacing, the submersible was then towed to another dive location, where the process was repeated. A total of 17 ascents were completed during the 8 dives.

Ascent speed varied according to habitat complexity, slope, and crustacean abundance, but was slow enough to permit recording of the species observed except in areas where extremely dense concentrations of animals were found. Observers were stationed on opposite sides of the submersible, with no overlap in their visual field. Each observer was able to scan approximately 90° on one side of the submersible's path.

As discussed by Richards and Schnute (1986), a general problem with use of submersibles has been the quantification of species abundance. Both the presence of lights and the submersible itself might affect animal behavior and hence bias observations. Prawns tend to be cryptic and were frequently found in association with bottom debris, and occasionally in holes. After extensive observations, including moving at specific locales with lights on or off and moving at variable speeds, it was concluded that prawns and other demersal crustaceans were not apparently affected by *Pisces*'s presence, allowing them to be effectively studied. On the approach of *Pisces*, demersal crustaceans would occasionally swim a short distance with rapid flicks of their abdomens, but in most cases, they would simply assume an aggressive stance towards the submersible and continuously face it as it passed by. They did not retreat under cover.

Visibility of benthic animals varied somewhat because of changes in bottom topography and its effect on distance of the submersible from the substrate. Water clarity was generally good (>7 m), but resolution was poor at the perimeter of the illuminated area (about 5 m maximum).

Data were initially recorded into handheld tape recorders, and tapes were transcribed shortly after each dive. Prawns were individually counted and their depths of occurrence noted over a vertical transect of about 3 m. However, this procedure could not be used when live prawn abundance exceeded approximately 6 m^{-2}, because of their high density and because the prawns stirred up the substrate by their movements. This situation only occurred over a narrow depth range (between 70 and 85 m depth, depending on date of observation). Dead prawns, which often only consisted of exoskeleton fragments, were also difficult to count at a density greater than about 2 m^{-2}. In both situations, number per meter of depth was conservatively estimated by multiplying the respective minimum average density per square meter by 3 m, the transect width over which live and dead prawn abundances were being assessed.

Qualitative notes on abundance of munids, *Munida quadraspina* Benedict, 1902, the dominant benthic crustacean present, were recorded by depth interval. Observers noted other invertebrate and fish species present in each transect.

Movement of observed crustaceans was sufficiently slow, relative to the submersible's movement, to prevent their crossing the submersible's path and possible double counting by the observers. Body size of some individuals was estimated by comparing them to a 30 cm rod, marked in 10 cm intervals, that hung in front of the left viewport. Sizes were later confirmed by measurement of carapace lengths of specimens collected using the extendable arm of the submersible.

Water samples, and on some occasions crustaceans, were collected at selected depths by pumping water through jars attached to the exterior of the submersible until they had been thoroughly

flushed, and then sealing them. Samples were fixed with manganous sulphate reagent and alkaline iodide solution as soon as the submersible had surfaced and was recovered at the end of each dive, and dissolved oxygen concentrations were determined later using a modified Winkler titration procedure (Strickland and Parsons 1972). Ambient water temperature was recorded continuously during each dive. On 14 October 1986, a more comprehensive set of oceanographic measurements (temperature, salinity, and dissolved oxygen [DO_2]) was obtained by University of British Columbia (UBC) oceanographers 1 km from the study area.

Results

Substrate type was a soft, light-brown flocculent ooze at the bottom of the inlet up to a depth of about 60 m, when it became more gravelly. The floor of the inlet was relatively flat, changing to a slope of 30–60° at the walls up to a depth of about 100 m, at which point 5–10 m vertical rock cliffs often occurred. The slope then lessened at approximately 70 m depth to 20–30°, with frequent rock outcroppings observed up to the minimum depth (20 m) surveyed.

Salinity and temperature below 20 m ranged from 30.0 to 31.4‰ and from 8.0° to 11.2°C, respectively, throughout the study. During the first two days of observations, measured DO_2 levels were >1 mL · L^{-1} at depths above 20 m. Between the afternoon and evening dives of the third day (8 October), an abrupt decrease in DO_2 concentration to between 0.76 and 0.92 mL · L^{-1} was detected at depths of 75–77 m. However, at nearby depths of 71–73 m, DO_2 levels remained above 1 mL · L^{-1} (1.29–2.00 mL · L^{-1}).

Dissolved oxygen (DO_2) measurements obtained during the last two days of our study show a similar profile to those obtained four days later in the center of the inlet by the UBC team (Fig. 1). In both cases, a region of low DO_2 (<1 mL · L^{-1}) was seen in waters of intermediate depth, although the depth at which this lens of low DO_2 occurred differed by about 20 m. Minimum DO_2 level recorded during our dives was 0.76 mL · L^{-1} at 77 m on 8 October, while on 14 October in the center of the inlet, the lowest value noted was 0.44 mL · L^{-1} at 110 m. Since low DO_2 levels normally occur in the deepest waters of the inlet (Pickard 1975; Burd and Brinkhurst 1984), these results indicated that there had recently been intrusions of denser, more oxygenated water over the sill into the deeper regions of the inlet, displacing the low DO_2 layer upwards or advecting low DO_2 water into the study area.

There were clear differences in depth ranges inhabited by species commonly observed in the study area (Fig. 1). The species we observed were primarily benthic in habit, although some epibenthic species such as spotted ratfish, *Hydrolagus colliei* (Lay and Bennet, 1839); spiny dogfish, *Squalus acanthias* Linnaeus, 1758; and Pacific cod, *Gadus macrocephalus* Tilesius, 1810, were periodically observed, usually at depths below 80 m. Various rockfish (*Sebastes* sp.) were observed around rock outcroppings.

The most abundant benthic invertebrate species observed below 60 m were four species of shrimp (*Spirontocaris holmesi* Holthuis, 1947; *S. sica* Rathbun, 1902; pink shrimp, *Pandalus jordani* Rathbun, 1902; and prawn) and munids. A few Dungeness crab, *Cancer magister* (Dana, 1851) were observed at 40–80 m depth. Greatest densities of prawns generally occurred between 70 and 85 m depth, although their observed range was from 20 to 159 m (Table 1). There was no obvious difference in the depth range of major prawn concentration (70–85 m) between afternoon and night dives on the same day. However, more prawns were observed in the depth range of 20–70 m at night than during the day, but these were relatively few in comparison to those at 70–85 m depth (Table 1). During the latter part of the study, most prawns were in a narrow band between 70 and 79 m depth. An amphipod, *Orchomene obtusa* (Sars, 1890), was common on the substrate from 80–210 m water depth. Major concentrations of pelagic amphipods were observed at depths of 45–75 m and 23–90 m during the day and night, respectively. Euphausiids were most abundant at 90–135 m during the day and at 50–90 m at night.

Munids were not observed above the main prawn concentration at 70–85 m. A wide size range of munids was observed, ranging from recently settled juveniles to adults of about 3 cm carapace length. In general, large individuals were found below 100 m whereas small munids were found from 80 to 120 m depth. Munids were observed down to the deepest depth surveyed (209 m).

On the evening dive of the third day, 8 October, dying and dead prawns, the latter covered with swarms of amphipods, were observed between 82 and 90 m depth, with most between 85 and 90 m (Table 1). Some live prawns showing disoriented behavior were also observed. Examination of collected live prawns observed to be in poor condition when sampled showed no evidence of disease or

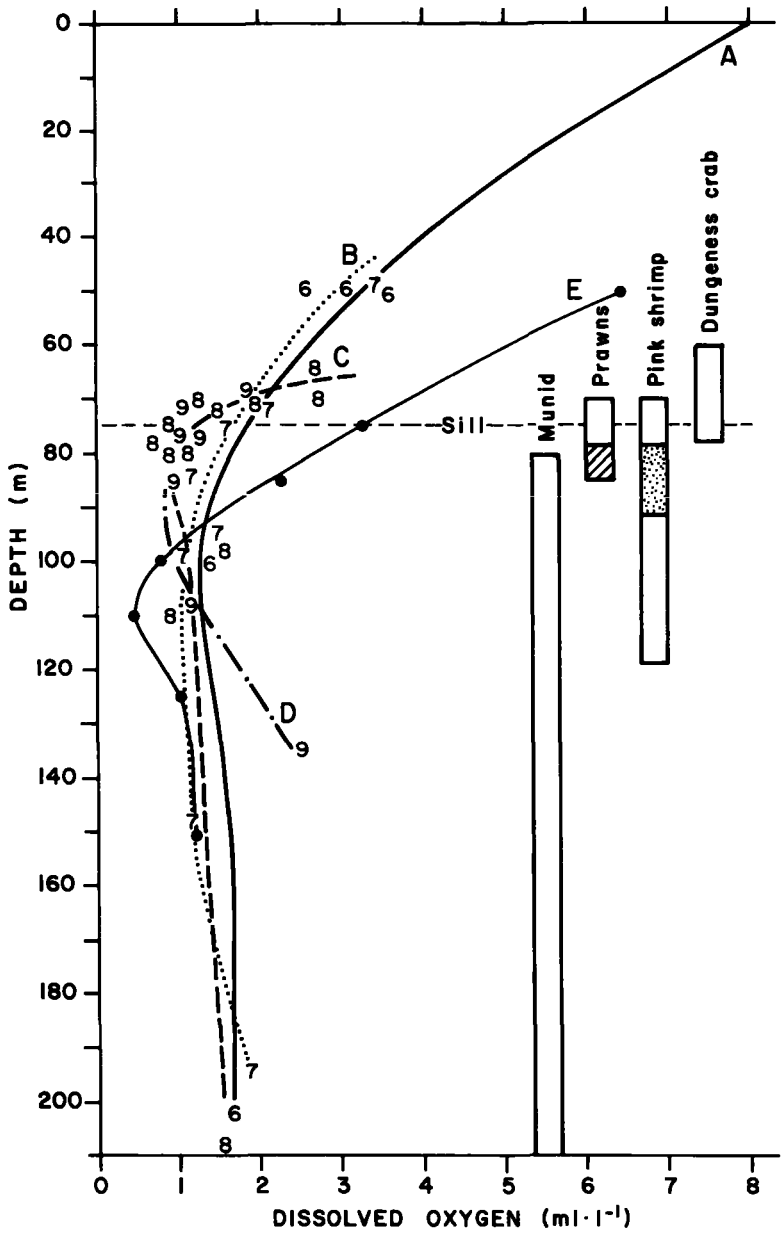

FIGURE 1.—Dissolved oxygen levels (mL · L^{-1}) at depth during each of the 4 days of diving (lines were drawn by eye) and for the UBC sampling, and relative depth distributions of the main abundances of the four large crustaceans observed. Oblique bar = zone of prawn mortality; stipple = area devoid of pink shrimp after low DO_2 water intrusion. Numbers = dates in October 1986. A (——) = 6 October, B (•••) = 7 October, C (– – –) = 8 October, D (–•–•) = 9 October, E (•—•) = 14 October (UBC profile).

TABLE 1.—Average prawn abundance per observer per 5 m depth increment observed in the depth range 20–124 m during the 4 days of observations, 6–9 October 1986. A = afternoon dive, E = evening dive, numbers in brackets = no. of ascents, no. of observers, < > = dead or dying.

	6 October		7 October		8 October		9 October	
Depth (m)	A (2,1)	E (2,2)	A (1,1)	E (2,1)	A (1,1)	E (3,2)	A (3,2)	E[1] (3,2)
20–24	0	0	0	1.5	0	0	0	—
25–29	0	0	0	1.5	0	0.5	0	—
30–34	0	0	0	3.5	0	0	0	—
35–39	0	0.25	0	4.5	0	0.5	0	—
40–44	0	1.00	0	2.5	0	2.0	0	—
45–49	0	2.0	0	2.0	0	0	0	—
50–54	0	2.5	0	0	0	0	0	—
55–59	0	7.0	0	0.5	0	0	0	—
60–64	0	10.0	1.0	1.0	0	0.5	0	—
65–69	0	14.25	0	5.0	0	1.0	0.6	3.0
70–74	1.0	[2]54.0	38.0	9.0	[2]80.0	2.0	[2]36.0	[2]80.0
75–79	[2]80.0	[2]80.0	0	[2]80.0	0	[2]80.0	[2]80.0 < 8>	[2]80.0
80–84	[2]80.0	[2]36.0	0	0	0	[2]16.0 <[3]18>	0 <[3]12>	[2]36.0 <[3]18>
85–89	0.5	1.0	0	0	0	0 <[3]30>	0 <[3]30>	0 <[3]30>
90–94	0.5	1.5	0	0	0	0 < [3]6>	0 <0.3>	0 <[3]12>
95–99	2.5	0.75	0	0	0	0	0	0 < 4>
100–104	2.0	0.75	0	0	0	0.3	0	0
105–109	2.5	2.75	0	0	0	0	0.25	0
110–114	3.0	4.25	0	0	0	0	0	0
115–119	2.0	0.25	1.0	0	0	1.0	0.25	0
120–124	0.3	1.5	0	0	0	0	0.25	0
Total alive	174.3	219.0	40.0	111.0	80.0	103.8	117.4	199.0
Total dead	0	0	0	0	0	54.0	50.3	64.0
Estimated mortality (%)	0	0	0	0	0	34	30	24

[1]No observations were made above 65 m on the evening of 9 October because of the entanglement of *Pisces* in submerged rope. Recorder equipment failure prevented inclusion of one of the observer's counts of prawn on some of the dives.
[2]Live prawn abundance was estimated >6 m^{-2}, but for purposes of analyses, 6 m^{-2} × 3 m^2 visibility was assumed, giving 18 prawn per meter of water depth.
[3]Dead prawn abundance was estimated >2 m^{-2}, but for purposes of analyses, 2 m^{-2} × 3 m^2 visibility was assumed, giving 6 dead prawn per meter of water depth.

parasitism (S. Bower[1]). Dead prawns, sometimes consisting only of exoskeleton remains, were observed at a density >2 m^{-2} in some areas. Apparently healthy prawns were concentrated in the depth range of 75–80 m at densities >6 m^{-2}. Dead and dying prawns were also observed during both dives on 9 October. By comparing the estimated numbers of dead and living prawns observed in a vertical transect, it was conservatively estimated that approximately 25% of the prawn population observed may have died during this 24-h period, with observations taken over 9 ascents along about 1.5 km of shoreline (Table 1).

Prawn was the only species observed to be dying. Apparently healthy amphipods, munids, and flatfish were observed around the dying prawns. However, coincident with the onset of prawn mortality, the vertical distribution of pink shrimp separated into two groups, one above and one below the depth range of prawn mortality (Fig. 1). No dead pink shrimp were observed. Only amphipods were observed eating the dying or dead prawns.

Discussion

Our observations indicate that the tolerance of prawn to low DO_2 levels may be less than that reported from laboratory experiments. The tolerance of prawn in a sealed chamber (10°C, 30‰ salinity) to low DO_2 levels has been experimentally examined by Whyte and Carswell (1982). Under their experimental conditions, prawns exhibited a reduced metabolic rate at DO_2 levels below approximately 2.5 mL · L^{-1} and died at approximately 0.35 mL · L^{-1}. They did not determine how long prawns would survive at dissolved oxygen levels below 1 mL · L^{-1} since their experimental design included only a fixed amount of oxygen. Our study suggests that minimum tolerance occurs at around 1 mL · L^{-1} since at levels below this, death occurred. Oxygen stress in munids has been reported (Burd 1983) to coincide with a loss of equilibrium similar to the disoriented locomotor behavior we observed for

[1]S. Bower, Pacific Biological Station, Nanaimo, B.C., V9R 5K6, pers. commun. October 1986.

prawns. Based on our observations, we further note that prawns appear to be less tolerant to low DO_2 levels than many of the other species found in the same depth range. However, published data on tolerance to hypoxic conditions for the species present exists only for munids, which have been shown to tolerate hypoxic conditions as low as 0.1–0.15 mL · L^{-1} (Burd 1983; Burd and Brinkhurst 1984, 1985).

All benthic species observed, except prawn, had a relatively large depth range over which individuals were found in abundance. Those species apparently more tolerant to low DO_2 levels were found from about 85–210 m. It is unknown why in contrast to other species observed, prawns were concentrated in a narrow depth range at 70–85 m water depth, so close to lethal water conditions. Most prawns were apparently prevented from going deeper by intolerance to low DO_2 concentrations, although a few individuals were below this low DO_2 layer and, for the short term at least, were apparently surviving. At night, there was little change in the observed general depth preference of the main prawn concentration, although more prawns were observed at shallower depths. Prawns were not observed moving vertically on the cliffs in a directed manner, and so prawns observed at shallower depths at night may have been hidden there during the day.

With the sudden movement of low DO_2 water into the depth range occupied by prawns, it is unknown why prawns did not simply walk upwards on the cliff, away from the low DO_2 area, and stay in a tolerable environment, as did the pink shrimp. The distance prawns would have had to travel was <10 m in the 70–75 m depth range. Some vertical movement of prawns may have occurred, since in the afternoon dive prior to the evening dive in which dead prawns were first observed, the depth range in which prawns were abundant was narrow (5 m) and at its shallowest depth (70–75 m).

Two oceanographic factors apparently caused the observed prawn mortality: the existence of a low DO_2 water mass in close proximity to the prawns and some event which caused this water mass to intrude suddenly into the prawn habitat. As indicated earlier, the presence of oxyclines in Saanich Inlet is well documented, although the close proximity of prawns to this lethal environment had not previously been described.

We offer two possible explanations that could account for sudden intrusion of the anoxic layer: 1) change in the amplitude of oscillations of the oxycline, or 2) an overall change in level of the mean oxygen surfaces, perhaps related to a change in subsurface properties. With respect to the first, Thomson et al. (in press) showed that in Saanich Inlet, there are regular, peak-to-peak oscillations in DO_2 level of the order of 2.5 mL · L^{-1} at 100 m depth. These oscillations were found to occur over a period of hours, with a standard deviation and range of effective vertical isopycnal displacement estimated to be 2.0 and 9.6 m, respectively. Thomson et al. (in press) collected their data in April 1987, when the mean DO_2 level at 100 m was 4.8 mL · L^{-1}. If similar oscillations of the oxycline occurred during our observations, when DO_2 levels were much lower, then with a moderate change in oscillation amplitude, prawn could suddenly experience lethal DO_2 levels for time periods up to approximately 6 hours. The causal mechanism generating the oscillations and changes in amplitude of oscillation of the pycnocline, and hence oxycline, is currently unknown, but is probably due to internal gravity waves propagating within the inlet (R. Thomson[2]).

The second explanation involves a rapid change in average depth of the oxycline caused by changes in vertical density profile of the water column. Intermediate depth waters outside Saanich Inlet are most dense in the fall, and intrusion of this denser water over the sill into the inlet typically occurs at this time (Pickard 1975). Such intrusions are often caused by strong tidal influxes, and fluctuations in depth of the pycnocline and oxycline subsequently propagate down the inlet as a density intrusion (Holbrook and Halpern 1982). Any intrusion has the potential of suddenly altering oxygen concentrations at various depths. The observation of mortality beginning in late afternoon on 8 October is in agreement with that expected based on the daily and hourly timing of tidal action seen during the study period.

Prawn mortality as described would thus appear to be an episodic, but perhaps not an uncommon, event in Saanich Inlet. It is probably a fall phenomenon, for the oceanographic reasons described above and since in other years, this was when the hypoxic layer was shallowest (Richards 1965; Tunnicliffe 1981; Burd and Brinkhurst 1984). Our observations clearly demonstrate that sudden catastrophic mortality can occur on a scale which may noticeably affect species abundance in an area. If undocumented, such episodic mass mortality may confound an understanding of species population dynamics. For fishermen in the area, mortality of prawn is a concern and may explain why seasonal landings may

[2]R. Thomson, Institute of Ocean Sciences, Sidney, B.C. V8L 4B2, pers. commun. May 1987.

not meet expectations. Understanding the timing and likelihood of such events can improve management, and since the geographical occurrence of such mortality may often be quite localized, increased harvest in specific locations prior to high natural mortality events might be justified.

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MORPHOLOGICAL DIFFERENCES BETWEEN TWO CONGENERIC SPECIES OF PLEURONECTID FLATFISHES: ARROWTOOTH FLOUNDER, *ATHERESTHES STOMIAS*, AND KAMCHATKA FLOUNDER, *A. EVERMANNI*

The two flatfishes of the genus *Atheresthes* (family Pleuronectidae) are commonly caught in the eastern Bering Sea commercial trawl fishery. From 1977 to 1983, they comprised an estimated 10.03% of the total flatfish catch by the foreign trawl vessels in the Bering Sea/Aleutian Islands region (data compiled from U.S. Foreign Fisheries Observer Program, Northwest and Alaska Fisheries Center). However, these two species, the arrowtooth flounder, *A. stomias*, and Kamchatka flounder, *A. evermanni*, are morphologically similar and hence difficult to distinguish. As a result, fisheries workers in the field often lump the two species or misidentify them. Because the two species may have biological differences not presently known, it is important for management considerations and stock assessments to distinguish the species in fisheries surveys. The objective of this paper is to describe gross morphological differences between the two species more explicitly, so that the two can be accurately identified in the field.

Norman (1934) thought that these two species of *Atheresthes* were so similar that eventually they were shown to be identical. However, based on electrophoretic evidence, Ranck et al. (1986) concluded that *A. stomias* and *A. evermanni* are valid species. Wilimovsky et al. (1967) previously had reached this same conclusion by using a special morphological character index to separate the two species. This index is a function of caudal vertebrae number, gill raker number, distance from anterior eye margin to dorsal origin, and eye diameter. Unfortunately, the index is too complex to use in the field because it is based partly on characters that cannot easily be evaluated by gross external examination. This study describes a simpler method for differentiating the two species based on previously described external morphological characteristics and two new morphological characters.

Methods

Collections were made in the eastern Bering Sea in an area between lat. 54° and 59°N, long. 163° and 174°W (Fig. 1) aboard the National Marine Fisheries Service RV *Chapman* in summer 1984.

Specimens were unselectively sampled in the field from trawl catches containing *A. stomias* and *A. evermanni*. The fork length and sex of the fish along with location of sample were recorded, and each specimen was preserved in 3.7% seawater/formaldehyde solution.

In the laboratory, the following characteristics were examined:

1) Upper eye position: Specimens were first classified according to the position of the upper eye, following Norman (1934). If the orbit of the upper eye interrupted the profile of the head (Fig. 2A), the specimen was classified as *A. stomias*. If the upper eye did not interrupt the profile of the head (Fig. 2B) and was completely on the right side of the head, the specimen was classified as *A. evermanni* (Norman 1934; Wilimovsky 1967).

2) Gill raker counts: After initial separation of the specimens on the basis of the upper eye position, the four gill arches of the eyed side were removed and the gill raker count of each of the four arches recorded. Counts of the upper and lower limbs were recorded separately and the two counts were separated by a plus sign (for example, 4+12 means 4 rakers on the upper limb and 12 on the lower limb). If a gill raker straddled the angle of the arch, it was included in the count of the lower limb. In this study, only the lath-shaped structures were counted as gill rakers; the rudiments were not counted.

Results

A total of 251 fish was examined. Based on the upper eye position, 170 specimens were classi-

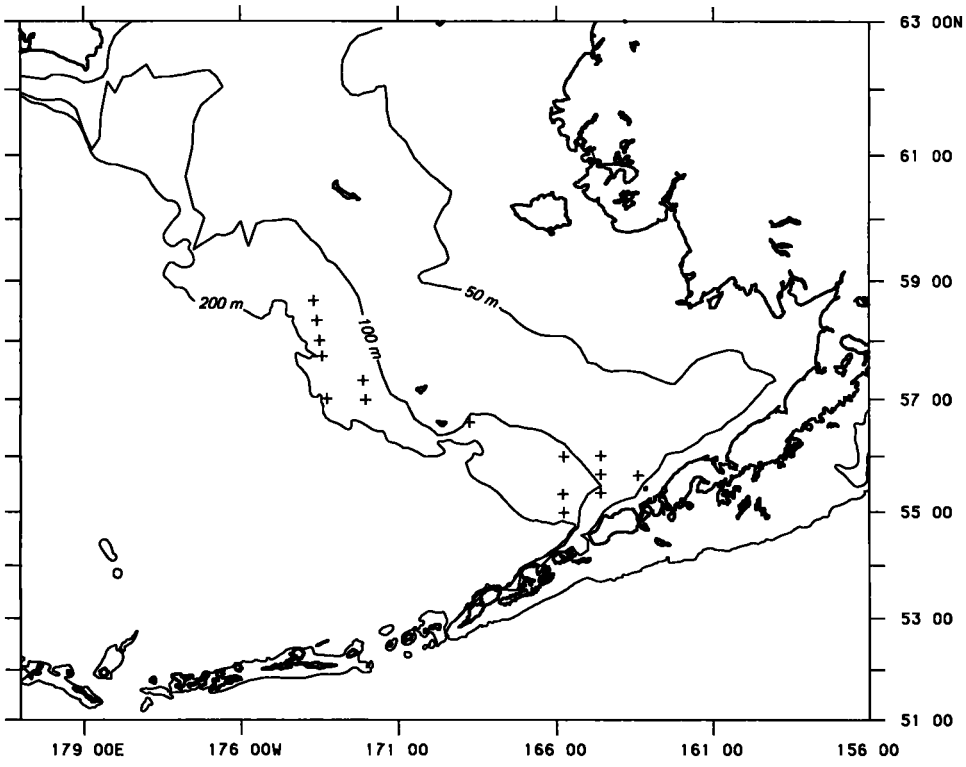

FIGURE 1.—Bering Sea collecting localities.

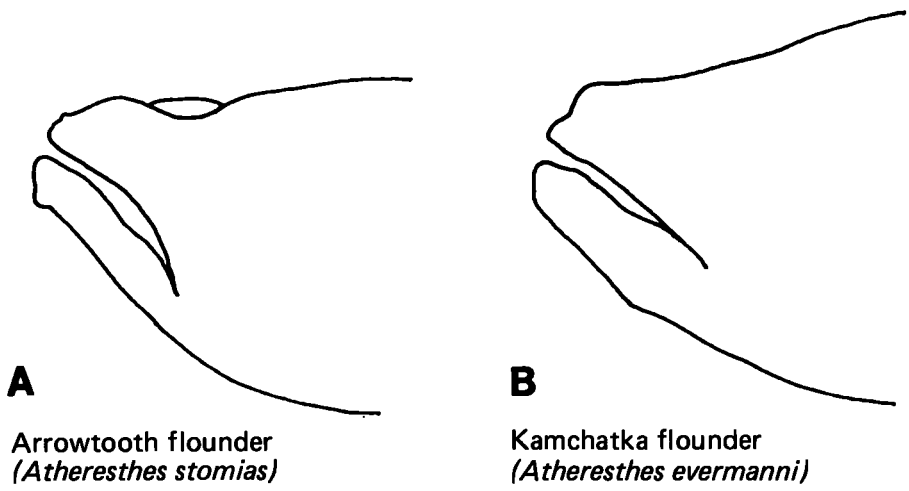

FIGURE 2.—Blind side view of head profiles of *Atheresthes stomias* (A) and *A. evermanni* (B).

fied as *A. stomias*, and 81 as *A. evermanni*. Gill rakers decreased in number from the first to the third gill arches in both species. Neither species had gill rakers on the fourth gill arch (though they did have rudiments).

First Gill Arch

In general, *A. stomias* had more gill rakers (on both the upper and lower limbs) on the first gill arch than did *A. evermanni*; however, the counts did overlap both in arrangement of gill rakers and total numbers (Table 1). Of the *A. stomias* examined, 75.2% had 4 or more rakers on the upper limb and none had fewer than 3. On the other hand, no *A. evermanni* had 4 or more gill rakers, and 49.4% had 2 rakers on the upper limb on the first gill arch.

Second Gill Arch

As was the case of the first gill arch, *A. stomias*, in general, had more gill rakers on the second gill arch than did *A. evermanni*. There were minor overlaps (1.8%) between these two species in the total gill raker counts and in the distribution of the gill rakers (Table 2). In addition to having different gill raker counts and patterns, all of the *A. evermanni* examined had 1 gill raker on the upper limb of the second gill arch, whereas 98.2% of the *A. stomias* had 2 gill rakers on the upper limb of the second gill arch (Table 2).

Third Gill Arch

In general, *A. stomias* had more gill rakers on the third gill arch than did *A. evermanni*. The range of total raker counts for *A. stomias* was 3 to 7, with most (85.3%) having 4 or 5. Total raker counts for *A. evermanni* ranged from 2 to 5, with 64.2% having 3. The most frequent arrangements of gill rakers on the third gill arch of *A. stomias* were 0+4 (43.5%) and 0+5 (41.2%), and the most frequent arrangement for *A. evermanni* was 0+3 (64.2%). Only three (1.8%) *A. stomias* had one gill raker on the upper limb of the third gill arch. The rest (98.2% *A. stomias* and all *A. evermanni*) had no gill rakers on the upper limb of the third gill arch.

Anomalous Specimens

Three specimens had the upper eye interrupting the profile of the head but had only 1 gill raker on the upper limb of the second gill arch. These fish were probably *A. stomias* with anomalous gill raker counts. One of the three had gill raker patterns of 4+11, 1+9, and 0+4 on the first, second, and third gill arches, respectively. The gill raker patterns on the blind side of this specimen were 3+11 on the first gill arch, 2+9 on the second, and 0+4 on the third. Thus, because this specimen had 4 gill rakers on the upper limb of the first gill arch on the eye

TABLE 1.—Gill-raker arrangements and their percentages (%) of frequency of occurrence (FO) on the first gill arches (eyed side) of *Atheresthes stomias* and *Atheresthes evermanni* collected from eastern Bering Sea.

	stomias		*evermanni*	
Pattern	FO	%	FO	%
5+11	2	1.2	0	0
4+13	1	0.6	0	0
4+12	59	34.7	0	0
4+11	65	38.1	0	0
4+10	1	0.6	0	0
3+13	1	0.6	0	0
3+12	11	6.5	0	0
3+11	29	17.1	4	4.9
3+10	1	0.6	32	39.5
3+9	0	0	5	6.2
2+11	0	0	3	3.7
2+10	0	0	29	35.8
2+9	0	0	8	9.9
Total	170	100	81	100
Mean	15.1		12.4	

TABLE 2.—Gill-raker arrangements and their percentages (%) of frequency of occurrence (FO) on the second gill arches (eyed side) of *Atheresthes stomias* and *Atheresthes evermanni* collected from the eastern Bering Sea.

	stomias		*evermanni*	
Pattern	FO	%	FO	%
3+10	1	0.6	0	0
2+11	3	1.8	0	0
2+10	54	31.8	0	0
2+9	108	63.4	0	0
2+8	1	0.6	0	0
1+9	3	1.8	8	9.9
1+8	0	0	61	75.3
1+7	0	0	11	13.6
1+6	0	0	1	1.2
Total	170	100	81	100
Mean	11.3		8.9	
2 or more rakers on upper limb	167	98.2	0	0
1 raker on upper limb	[1]3	1.8	81	100

[1]All of these *A. stomias* have two gill rakers on the upper limbs of the second gill arches of the blind side. Their patterns are either 2+10 or 2+9.

side and 2 gill rakers on the upper limb of the second gill arch on the blind side, it is referred to *A. stomias*. The other two anomalous specimens also had 2 gill rakers on the upper limbs of the second gill arch of the blind side and were also recorded as *A. stomias*.

Discussion

From this study, it is evident that the two species of *Atheresthes* can most easily be distinguished by eye position. The number of gill rakers on first and second gill arches can be used to assist and verify identification.

When identifying specimens, eye position should be examined first. If the upper eye interrupts the profile of the head, this specimen is *A. stomias*; if the upper eye does not interrupt the profile of the head, the specimen is *A. evermanni*. If the head is in bad shape (e.g., damaged during the trawl operation) or if the examiner has difficulty using eye position and head profile to identify a specimen, the gill arches must be examined. Two or more gill rakers on the upper limb of the second gill arch indicates that the specimen is *A. stomias*; if there is only 1 gill raker, the specimen is *A. evermanni*.

The number of gill rakers on the first gill arch has generally been used to distinguish the two species of *Atheresthes*. However, this study demonstrated a greater overlap between the two species in number of rakers on the first gill arch than the second gill arch (Tables 1, 2), indicating that the second gill arch is a better character for assigning individuals to the species.

The study also suggests that the number of gill rakers on the upper limb of the first gill arch is species specific. If there are 4 or more gill rakers, the specimen is *A. stomias*; 2 or fewer gill rakers indicate the specimen is *A. evermanni*.

The uncertainty in examining the first gill arch is when there are 3 gill rakers on the upper limb. Approximately 25% of *A. stomias* and 50% of *A. evermanni* samples had 3 gill rakers on the upper limb of the first gill arch. Thus, when 3 gill rakers are present on the upper limb of the first gill, the second gill arch must also be examined to distinguish the two species.

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PREDATION OF KARLUK RIVER SOCKEYE SALMON BY COHO SALMON AND CHAR

The number of sockeye salmon, *Oncorhynchus nerka*, in Alaska's Karluk River (Fig. 1) declined from millions to thousands during the early part of the present century. Rounsefell (1958) discussed alternative explanations for the decline including a general loss of fertility of the system as the number of salmon carcasses declined, competition, overfishing, subtle changes in climate, and predation; he concluded that the combined effect of predation and fishing was the most probable explanation. Later, Van Cleave and Bevan (1973) suggested that the weir constructed in the river each year to facilitate counting the fish as they entered the system was the most probable cause of the decline. It prevented free movement of both adults and juveniles in the river. All of these hypotheses remain as potential explanations for the decline.

Fredin et al. (1974) described a relation that showed two equilibrium regions between the spawning stock and the resultant run for sockeye salmon in the Kodiak area. We developed a stock-recruitment curve (Fig. 2) for sockeye salmon in the Karluk River basin that also showed two equilibrium regions, and suggested that the population had "col-

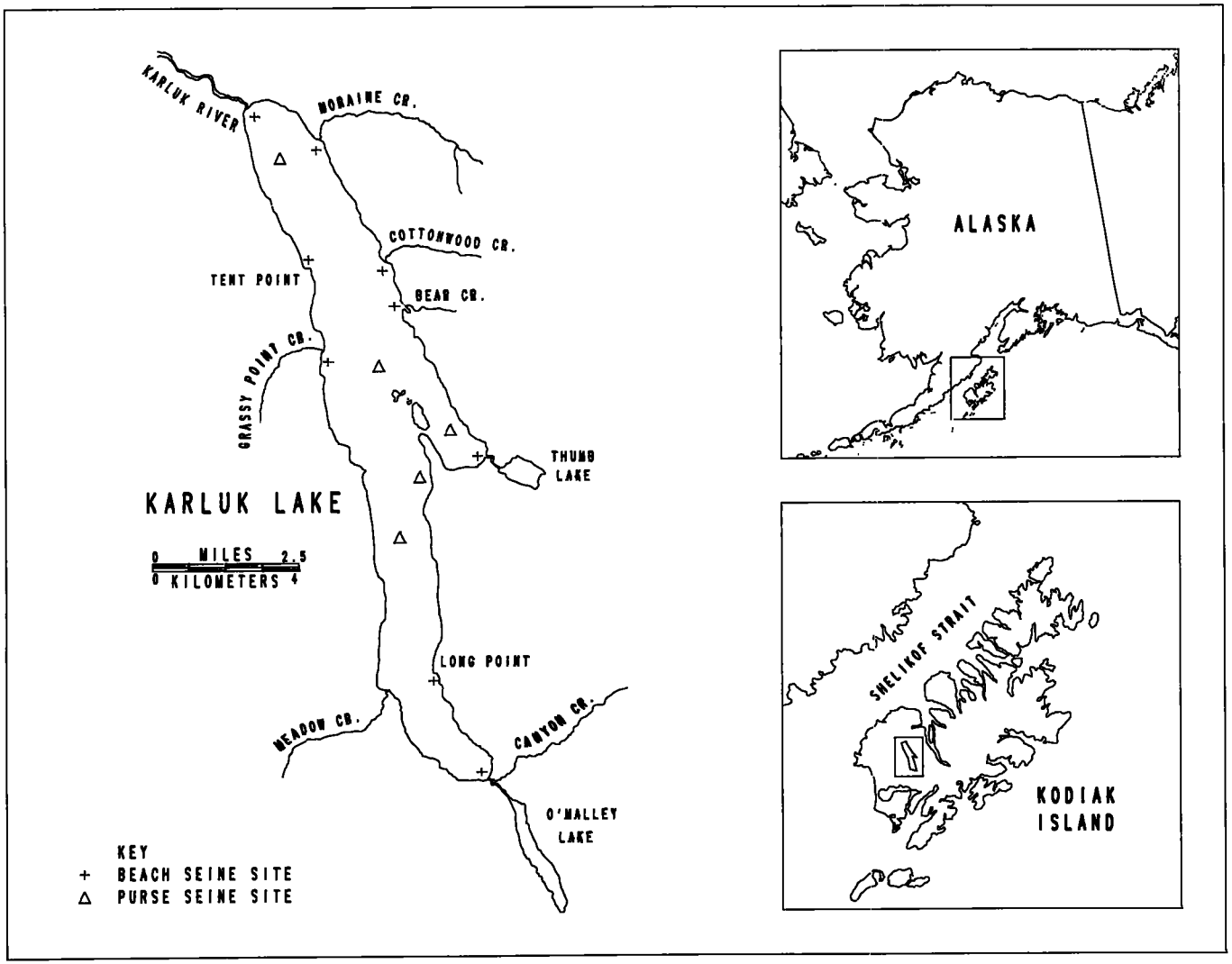

FIGURE 1.—Karluk Lake and associated waters, and sampling sites for a predation study.

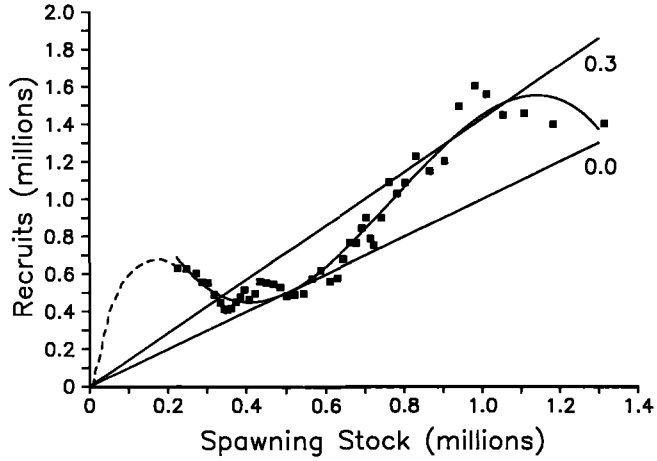

FIGURE 2.—Stock-recuit relation for sockeye salmon in the Karluk River basin. Squares are the running geometric mean (by 9) of stock and recruit estimates for the 1922–77 broods. The curved, solid line was described by $R = 1.83(10^6) + 7.73P + 1.29(10^{-5})P^2 - 5.58(10^{-12})P^3$; where, R = recruits and P = stock. Ages of fish in the escapement (1922–36 from Barnaby 1944; 1937–69 from the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, Auke Bay, AK; 1980–85 from Alaska Department of Fish and Game, Kodiak, AK) were used to estimate the recruits produced by each brood. The diagonal lines show how the replacement line changes as the exploitation rate increases from 0 to 0.3.

lapsed" into the lower of the two. Fishing can cause such a collapse (Peterman 1977) and recovery becomes impossible unless exploitation rates are reduced to levels substantially lower than the rate that caused the collapse.

Multiple equilibria in an exploited population can be caused by depensatory mortality—the loss of a relatively greater fraction of the population when it is small than when it is large (Neave 1953). Several functional responses (Ricker 1954; Holling 1973) have been used to describe relations between prey density and predation rate—one of which (Type III relation) can produce multiple equilibria in the stock-recruitment curve of a prey population (Peterman 1977). The Type III or S-shaped functional response is characteristic of predators that consume a small fraction of the prey at low prey population density; as prey population density increases, however, the predators rapidly increase the fraction consumed through learning or aggregation. The concave, Type II functional response holds when the fraction consumed is high at low prey density.

The apparent potential for stock collapse, as depicted in the Karluk sockeye stock-recruitment curve, could be the consequence of Type III predation mortality. A preliminary survey of the food habits of fish in the system showed that coho salmon, *O. kisutch*, and two chars—the Dolly Varden, *Salvelinus malma*, and Arctic char, *S. alpinus*—were predators of juvenile sockeye salmon. We set out to determine whether the functional responses for coho salmon and for char were of Type II or Type III. Our approach was to describe the relation between the number of prey eaten per predator and the index of prey abundance provided by the annual counts of adult sockeye salmon that entered the system for spawning. Unfortunately, the study had to be terminated after five years because of a management decision to enhance the productivity of Karluk Lake with commercial fertilizer; we could not eliminate the possibility that the effects of fertilization would confound predation responses. We describe the data that were accumulated during five field seasons and our tentative conclusions concerning the role of predation mortality in the dynamics of these sockeye salmon.

Methods

Sampling sites were established at locations around the littoral zone of Karluk Lake at the outlets of spawning streams and at beach spawning areas (Fig. 1) in 1982. The Karluk River was sampled from the outlet at the lake to about 100 m downstream.

In each of the five subsequent years, a field crew sampled each location at weekly intervals, from late April to October.

Juvenile coho salmon were collected with beach seines and minnow traps, and chars with beach seines, floating gill nets, and hook and line. Only coho salmon larger than 80 mm were found to be predators of sockeye salmon during the April–October sampling period. Since char were captured with hook and line or in gill nets, our samples contained only fish that were large enough to consume sockeye salmon fry. Coho salmon were preserved in formalin for examination later, when the contents of the stomachs were removed and the sockeye salmon fry and fingerlings were counted. The chars were tagged and released after the contents were flushed from their stomachs and preserved in formalin.

Results

Juvenile coho salmon were aggregated around tributary outlets and in the littoral areas of Karluk Lake. The chars were found almost exclusively around the tributary outlets and in the Karluk River. Few coho salmon or chars were captured by seining in the pelagic areas of the lake. We did not distinguish between the two chars.

Predation rates for the chars did not increase as the abundance of sockeye salmon increased (Table 1), but the average number of sockeye salmon fry consumed by each coho salmon did increase and appeared to be depensatory (Fig. 3). A general equation (Real 1979) was used to describe the relation between the predation rate (Y) by coho salmon and the index of prey abundance (X),

$$Y = bX^c/(1 + aX^c). \quad (1)$$

A value of $c = 1$ provides a classic, Type II functional response curve, while values of c exceeding 1.0 provide a sigmoid, depensatory shape. A value of $c = 2$ gives the classic Type III curve.

Best (least squares) fit values for a, b, and c were obtained by transforming Equation (1) into the form

$$\ln(1/Y - a/b) = \ln(b^{-1}) - c\ln(X). \quad (2)$$

Using trial values of a/b, we regressed the left side of Equation (2) on $\ln X$ until we identified the value of a/b giving the lowest residual variance. The

TABLE 1.—Predation on juvenile sockeye salmon by predatory coho salmon (i.e., juvenile coho salmon longer than 80 mm) and chars in Karluk Lake, AK during June and July from 1982 to 1986.

	Coho salmon		Chars		
Year	Number examined	Predation rate	Number examined	Predation rate	Sockeye salmon escapement
1982	252	0.475	—	—	220,000
1983	3,132	0.076	95	0.98	164,000
1984	250	0.661	128	19.45	436,000
1985	956	0.452	485	10.06	420,000
1986	423	0.740	571	4.50	996,000

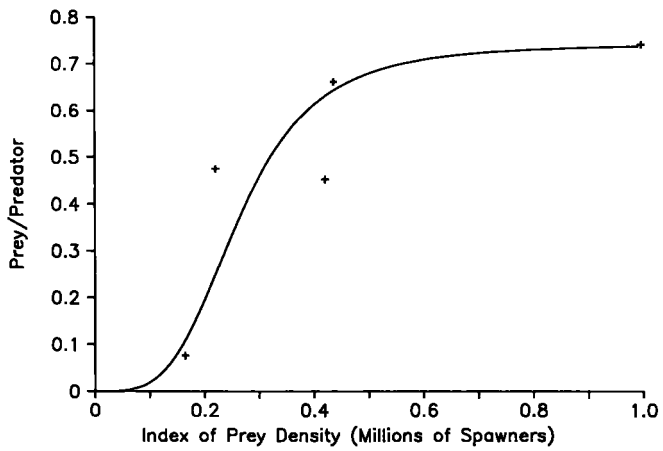

FIGURE 3.—Functional response curve for coho salmon greater than 80 mm (predators) and sockeye salmon (prey) in Karluk Lake. The index of prey abundance was divided by 1,000,000 (e.g. index 0.8 = 800,000 adults in the escapement).

results are $a/b = 1.35$, $c = 3.74$ (standard error = 0.79), $R^2 = 0.88$, $\ln(b^{-1}) = 46.98$.

Hence Equation (1) becomes

$$Y = bX^{3.74}/(1 + 1.35bX^{3.74}) : b = e^{-46.98}.$$

Inasmuch as Y ranges between zero and b/a, it seems unlikely that Y, or a corresponding statistical error term for Equation (1) would be approximated by a normal distribution. On the other hand, so long as Y does not rise above b/a (to which Equation (1) constrains it), the left side of Equation (2) lies between $-\infty$ and $+\infty$, and the error term is more likely approximated by a normal distribution. Consequently, we cautiously used the standard error associated with c, to test whether $c > 1.0$; that is, whether the functional response curve is sigmoid (Type III). In fact, c lies more than 3.5 standard errors above 1 (Type II response) and more than 2.2 standard errors above 2 (Type III response). Although the power of a test involving only 5 data points is weak, we feel that a tentative conclusion of depensatory predation by juvenile coho salmon is justified.

Discussion

Many adult salmon as they attempt to get to the spawning grounds, and as they spawn, are killed by Kodiak brown bears. Gard (1971) reviewed the available literature concerning predation of salmon by bears at Karluk and, in years when fish were not abundant, noted that bears had been observed to leave the salmon spawning areas to feed on berries in the local area, indicating that their predation also may be depensatory. We used data from Gard's summary to approximate the relation between the number of adult sockeye salmon in a run (X) and the number of unspawned adults (Y) estimated to have been killed by bears (Fig. 4). Although R^2 was only 0.424, a depensatory relation was indicated as $Y = X^{2.106}/(3102.85 + 0.00435X^{2.106})$; c, from Equation (1), was 2.106, with a standard error of 1.098. Because predation of sockeye salmon by bears, as well as predation by coho salmon, appeared to be depensatory, it is unlikely that predation by coho salmon alone was the sole cause of the complex stock-recruitment curve for sockeye salmon.

Prudent management of these salmon, and of salmon in systems similar to Karluk, may require regulation of harvest to prevent collapse of populations into relatively low equilibrium regions. Harvest levels that would have prevented collapse of the Karluk population can be estimated from the stock-recruitment curve (Fig. 2). An exploitation rate between 30 and 35% of the recruits should have maintained stock sizes associated with the upper equilibrium region. Exploitation at a constant rate of 0.40 increases the slope of the replacement line to the point that collapse of the population into the lower equilibrium region becomes inevitable (see Peterman 1977 for a description of the relation between the size of stability regions and exploitation rate). When depensatory mortality is potentially high for economically important populations, it may be necessary to limit exploitation to less than 35% of the recruits to prevent collapse.

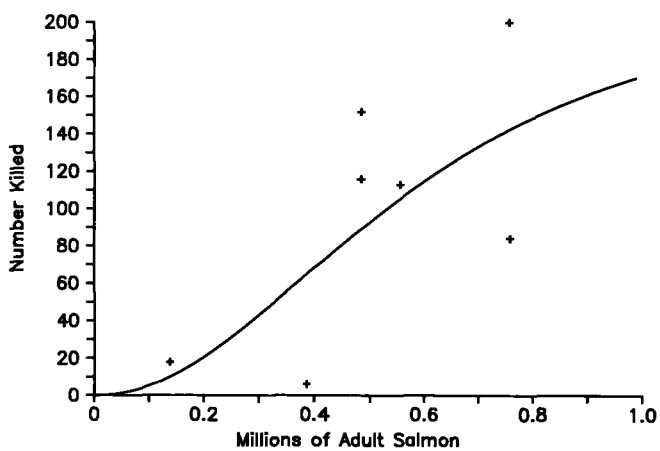

FIGURE 4.—Functional response curve for predation of sockeye salmon by bears. Number killed is thousands of unspawned salmon.

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We thank Jon Nelson for his support, and all others that participated in the project.

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SOME PROBLEMS IN ESTIMATING POPULATION SIZES FROM CATCH-AT-AGE DATA

ROY MENDELSSOHN[1]

ABSTRACT

A new method for estimating population sizes from catch-at-age data is given. The method treats the observed population sizes as missing data and uses a combination of the Kalman filter and the EM algorithm to derive maximum likelihood estimates of the parameters and minimum mean square error estimates of the population sizes. The algorithm does not assume that the observation errors and the errors in the population dynamics are uncorrelated with equal variances, which is a common assumption of existing techniques. A new parameterization for both recruitment and fishing mortality is given, based on smoothness priors. Recruitment (or fishing mortality) is estimated as a nonparametric function of time by calculating an "optimal" tradeoff between goodness-of-fit and smoothness of the function. The algorithm allows for multiple sources of observations (fishing, surveys, etc.) and allows for missing data in the observations, which can arise if the different sources of the observations occur on different time scales. An example suggests that the new algorithm may better capture variation that is important when using the population estimates to study the role of the environment (or other exogenous variables) on the population dynamics.

I can address the motivation of this paper by considering a slightly modified version of a model proposed by Collie and Sissenwine (1983). Assume that the underlying population dynamics satisfy

$$N(a+1,\ t+1) = [N(a,t) - C(a,t)]\ \tilde{m} + w(a,t)$$

$$a = 1,A \qquad (1)$$

where $N(a,t)$ is the number of fish age a at time t, $C(a,t)$ is the catch of age a fish at time t, $\tilde{m} = exp(-m)$ is the mortality rate and the vector $w(t) = (w(1,t), \ldots, w(A,t))^{\tau}$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix Q, and for any vector a, the notation a^{τ} denotes the transpose of the vector. We assume that the initial population vector $N(0)$ is gaussian with a mean of μ and covariance Σ.

The population itself is not observed. Instead we observe that

$$n(a,t) = q(t)N(a,t) + v(a,t) \qquad (2)$$

where q is an unknown parameter and the vector $v(t) = (v(1,t), \ldots, v(A,t))^{\tau}$ is a sequence of independent, identically distributed normal random vectors with mean 0 and covariance matrix R. It is assumed that $E(v(t)\ w(t)^{\tau}) = 0$; that is, the observation error and the underlying randomness in the population are uncorrelated. There is some interest in the value of the estimates of the $q(t)$ (or if mortality is to be estimated, in the estimate of $\tilde{m}$) but the major interest lies in estimating the unobserved population sizes $N(a,t)$. The estimates of the $N(a,t)$ should reflect not only the trend in the population, much as a regression might, but also the period-to-period variation of the population, such as might be related to environmental changes. This will be the emphasis throughout the paper.

The model described in Equations (1) and (2) differs from that of Collie and Sissenwine (1983) in that I do not assume that the mortality rate is known; here I allow the underlying population dynamics to be random, and the observation errors in Equation (2) to be additive rather than multiplicative. For known $\tilde{m}$, Collie and Sissenwine (1983) suggested minimizing

$$\sum_{t=1}^{T} \sum_{a=1}^{A} (v(a,t)^2 + w(a,t)^2) \qquad (3)$$

over the parameters (in our notation) $\theta = (q, N(t))$

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where $N(t)$ is the vector of unobserved population sizes. The concern here is not whether the multiplicative or additive form of the model is more correct, but rather what elements of the model are data, what are parameters, and how to calculate appropriate estimates of each.

If there were all-seeing observers, both the population process $N(t)$ and the observation process $n(t)$ would be available as data. Equations (1) and (2) imply a sequence of conditional probability distributions $f_N(N(t+1) \mid N(t), \theta_1)$ and $f_n(n(t) \mid N(t), \theta_2)$, where θ_1, θ_2 are parameters of the distributions to be estimated. Assuming additive gaussian errors, then θ_1 would include the mean vector $FN(t)$ and a covariance matrix that can be calculated recursively (see below). The mortality rate $\tilde{m}$ serves as a constraint on the form of the estimates of the mean vector, much as in the theory of regression. Similarly, the parameters for the observation process are a mean vector $H(t)N(t)$ and a covariance matrix, where $H(t)$ in this case depends on the parameters $q(t)$ that constrain the estimates of the mean vector. With an all-seeing observer, both $n(t)$ and $N(t)$ are realized values of random vectors and hence, are the data to be used to estimate the unknown parameters of the distributions, θ_1 and θ_2.

Thus, the unobserved population sizes are most appropriately treated as missing data. The estimation scheme proposed by Collie and Sissenwine (1983) treats the $N(t)$ as parameters to be estimated. Little and Rubin (1983, 1987: sec. 5.4) showed that treating missing data as parameters in likelihood equations does not produce maximum likelihood estimates of the parameters unless the proportion of missing data approaches zero as the sample size increases. This is because much of the asymptotic theory of maximum likelihood estimation depends on the number of observations becoming large, relative to the number of parameters. Little and Rubin (1983, 1987) showed that for a regression-like situation, the bias due to treating data as parameters can be quite large.

The alternate approach discussed by Little and Rubin (1983, 1987) is to integrate out the missing data from the complete data likelihood and maximize this function over the parameters as usually defined in estimation theory. This is the approach taken by Shumway and Stoffer (1982a), who used the EM (expectation-maximization) algorithm of Dempster et al. (1977) and Kalman filtering to derive maximum likelihood estimates for the parameters of the model and minimum mean square error estimates of the missing data.

I can explain some of the problems with estimating Equations (1) and (2), using the likelihood of Equation (3). Under the gaussian assumptions of the model, the complete data log-likelihood is given by (Shumway and Stoffer 1982a)

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}(N(0) - \mu(0))^{\mathrm{T}}\Sigma^{-1}(N(0) - \mu(0)$$

$$-\frac{T}{2}\log|Q| - \frac{1}{2}\sum_{t=1}^{T}(N(t) - FN(t-1))^{\mathrm{T}}Q^{-1}(N(t) - FN(t-1))$$

$$-\frac{T}{2}\log|R| - \frac{1}{2}\sum_{t=1}^{T}(n(t) - H(t)N(t))^{\mathrm{T}}R^{-1}(n(t) - H(t)N(t)) \quad (4)$$

where $F = \tilde{m}I$ and $H(t) = \mathrm{q}(t)I$. Similarly, the complete data log-likelihood in Equation (3) by substitution is

$$-\sum_{t=1}^{T}||N(t) - FN(t-1)||^2 + ||n(t) - H(t)N(t)||^2. \quad (5)$$

Collie and Sissenwine (1983) noted that their estimation scheme assumes that the process and observation errors have the same variance. However, from Equations (4) and (5) it can be seen that they make the stronger and unlikely assumption that both the errors in the population dynamics and the errors in the observation process are uncorrelated. Further, we can see from Equation (4) that when the $N(t)$ are treated as parameters, the estimates of the $N(t)$ depend on the observed data $n(t)$ for $t = 1,T$. Following Shumway and Stoffer (1982a), the expected log-likelihood conditioned on the observed data comprises three parts: a term due to estimating the expected value of the initial population size,

$$-\frac{1}{2}\log|\Sigma| - \frac{1}{2}tr\{\Sigma^{-1}[P(0|T) + (N(0) - \mu) \times (N(0) - \mu)^T]\}, \quad (6)$$

a term due to the unobserved dynamics,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|Q(t)| - \frac{1}{2}\sum_{t=1}^{T}tr\{Q(t)^{-1}[(N(t|T) - FN(t-1|T)) \times (N(t|T) - FN(t|T)^T + P(t|T) + FP(t-1|T)F^T - P(t-1|T) \times F^T - FP(t,t-1|T)]\}, \quad (7)$$

and a term due to the observation process,

$$-\frac{1}{2}\sum_{t=1}^{T}\log|R(t)| - \frac{1}{2}\sum_{t=1}^{T}tr\{R(t)^{-1}[(n(t) - H(t)N(t|T)) \times (n(t) - H(t)N(t|T))^T + H(t)P(t|T)H(t)]\} \quad (8)$$

where $N(t|s)$ denotes

$$N(t|s) = E[N(t) \mid n(1),\ldots,n(s)], \quad (9)$$

$P(t|s)$ denotes

$$P(t|s) = E[(N(t) - N(t|s)) \times (N(t) - N(t|s))^T \mid n(1),\ldots,n(s)], \quad (10)$$

and $P(t,t-1|s)$ denotes

$$P(t,t-1|s) = E[(N(t) - N(t|s)) \times (N(t-1) - N(t-1|s))^T \times \mid n(1),\ldots,n(s)]. \quad (11)$$

As shown in Equations (6) through (8), the proper estimates of the $N(t)$ and the related covariance matrices should be conditional expectations based on all of the data rather than on only the data up to time t. Assuming that all quantities are calculated properly, estimates that include only the data up to time $t-1$ are termed "predicted" estimates, estimates that include only the data up to time t are termed "filtered" estimates, while estimates given all the data are termed "smoothed" estimates. I shall show below that the appropriate formulas for predicted, filtered and smoothed estimates differ significantly. Thus using Equation (5) as the likelihood and treating the $N(t)$ as parameters does not produce proper estimates of the $N(t)$.

In the rest of this paper, I review state-space models and methods for estimating both the parameters and the unobserved components of the model. A very readable background for what follows is chapter 3 in Shumway (1988). The estimation scheme described does not require that the components of R, Q, and Σ have equal variance and are uncorrelated. Explicit estimates of these matrices are given. Then I show that a variety of age-based models proposed in the literature can be formulated as a state-space model, but that the formulations as presented make the same error of treating the unobserved components as parameters, and assume zero covariance in the errors. Auxiliary information as in Deriso et al. (1985) can be put into this format. And I show that the state-space formulation can include multiple observations of the population, but where some of the observations are missing. This can arise when the population is observed from fishing and from a variety of surveys, but some of the surveys are not done every year. This is essentially the problem discussed in Methot[2]. I give true maximum likelihood estimates for this model, allowing the different observation processes to have different error structures and estimate the relative weight that should be given each. This is a significant advance over the procedure in Methot (fn. 2).

A related paper is the analysis of Brillinger et al. (1980) who use a modified Kalman filter and maximum likelihood estimation to estimate the average birth and death rates and population structure of Nicholson's blow-fly data when only total numbers

[2]Methot, R. 1986. Synthetic estimates of historical abundance and mortality for northern anchovy, *Engraulis mordax*. Adm. Rep. LJ-86-29. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

of births and deaths at any time are available. In their model, knowing the births is equivalent to knowing the recruitment at each time period and the deaths are observed directly without error. Also, they appear to use the filtered estimates of the population structure, while the smoothed estimates are the minimum mean squared estimates given all the data. P. Sullivan[3] in his Ph.D. dissertation independently developed a length-based fishery model using Kalman filtering and maximum likelihood estimation.

I reiterate that the models considered here assume additive errors, while much of the existing literature prefers multiplicative errors, particularly for the observation equation. The basis of this preference appears to be that models with multiplicative errors have given a better "fit" to the data for other estimation schemes. In these estimation schemes the errors are assumed to have equal variances and are assumed to be uncorrelated. The better fit found for multiplicative errors in these algorithms may be due to these assumptions on the error variances. In effect, the errors are being scaled by the observed data which suggests that the assumption of equal variances is incorrect. In the present formulation I assume additive errors, but I can allow for errors with unequal variances, for errors that depend on the size of either the observed catch $n(a,t)$ or on the unobserved population $N(a,t)$, and for missing observations, and I can obtain simple to compute standard errors of the estimated underlying population sizes. The algorithm is also simple to program. If multiplicative errors are assumed, it is more difficult to calculate exact maximum likelihood estimates. Approximate likelihood methods (such as the extended Kalman filter) have known undesirable properties. When the full richness of the assumptions allowed in additive error models is used, it is an open question if multiplicative errors are to be preferred.

STATE SPACE MODELS

The State-Space Model can be written in the form (Jazwinski 1970; Anderson and Moore 1979; Ljung and Soderstrom 1983):

$$x(t) = F(t)x(t-1) + B(t)u(t-1) + Gw(t) \quad (12)$$

$$y(t) = H(t)x(t) + v(t) \quad (13)$$

where $x(t) = (x_1(t), \ldots, x_p(t))^T$ is the p-dimensional unobserved state of the system; $u(t) = (u_1(t), \ldots, u_p(t))^T$ is a p-dimensional vector of deterministic inputs; $y(t) = (y_1(t), \ldots, y_q(t))^T$ is the observed data of the system; $w(t) = (w_1(t), \ldots, w_p(t))^T$ is a sequence of zero mean normal vectors with common covariance matrix Q; $v(t) = (v_1(t), \ldots, v_q(t))^T$ is a sequence of zero mean normal vectors with common covariance matrix R; and F, B, G, and H are appropriately dimensioned matrices that may depend on an unknown parameter vector θ. Note that q, the dimension of the observation vector, can be larger than p, the dimension of the state vector. Thus several different observation processes of the underlying dynamics are allowed.

Using the same notation as in Equations (9) and (10), the predicted, filtered, and smoothed estimates of the state vector and the covariance matrices can be calculated recursively as follows: for prediction and filtering,

$$x(t|t-1) = F(t)x(t-1|t-1) + Bu(t-1) \quad (14)$$

$$P(t|t-1) = F(t)P(t-1|t-1)F(t)^T + GQ(t)G^T \quad (15)$$

$$K(t) = P(t|t-1)H(t)^T \times (H(t)P(t|t-1)H(t)^T + R(t))^{-1} \quad (16)$$

$$x(t|t) = x(t|t-1) + K(t) \times (y(t) - H(t)x(t|t-1)) \quad (17)$$

$$P(t|t) = P(t|t-1) - K(t)H(t)P(t|t-1) \quad (18)$$

where $x(0|0) = \mu$ and $P(0|0) = \Sigma$, and for smoothing,

$$J(t-1) = P(t-1|t-1)H(t)^T(P(t|t-1))^{-1} \quad (19)$$

$$x(t-1|T) = x(t-1|t-1) + J(t-1) \times (x(t|T) - x(t|t-1)) \quad (20)$$

$$P(t-1|T) = P(t-1|t-1) + J(t-1) \times (P(t|T) - P(t|t-1))J(t-1)^T. \quad (21)$$

The predicted state variable $x(t|t-1)$ differs from the quantity often used as the predicted value in the fisheries literature in that it is based on the last period's filtered estimate rather than on the last

[3]P. Sullivan, Center of Quantitative Sciences, University of Washington, Seattle, WA 98195, pers. commun. 1988.

period's predicted estimate. (For example, Deriso et al. (1985) suggested using backward VPA or cohort analysis to obtain predicted values.) The filtered estimate $x(t|t)$ is a weighted average of the predicted value of $x(t|t-1)$ and the observed error in estimating $y(t)$, where the weighting term $K(t)$ (the Kalman gain matrix) is regression-like. Similarly, the covariance of the estimate, as measured by $P(t|t-1)$, increases due to the prediction, but decreases by the amount $K(t)H(t)P(t|t-1)$ after the observation has been made. The smoothed estimate $x(t|T)$, which is the correct estimate of the underlying population (it satisfies the conditional expectation), is found by a backward recursion on the filtered estimates, where the filtered estimate is adjusted by a regression on the error between the smoothed and predicted estimates of the following period. Thus the smoothed estimates correct the predicted estimates both by the error in predicting the observed data as well as by the error in predicting the underlying population when using the filtered estimates of the underlying population. The square roots of the diagonal terms of the various P matrices produced by the Kalman recursions are the standard errors of the predicted, filtered, and smoothed estimates of the population.

Equations (12) and (13) are the basic form of the state-space model. It is a simple extension to the model to allow any of the matrices F, B, G, or H to be nonlinear functions of the past values of the $y(t)$ (see, for example, Shiryayev (1984), section VI.7), to allow the error vectors $w(t)$ and $v(t)$ to depend on past values of the $y(t)$ (Shiryayev 1984), or to allow the $v(t)$ to depend on the underlying state vector $x(t)$ (Zehnwirth 1988).

In a typical fisheries problem, the matrix $H(t)$ represents fishing. If some age-specific measure of effort $E(a,t)$ is known, then $H(t)$ is a diagonal matrix with $E(a,t)$ on the diagonals. Or it may be assumed that the exploitation rate is of the form $s(a)E(t)$, where $E(t)$ is known and the $s(a)$ values are to be estimated. Then for given values of $s(a)$, the matrix $H(t)$ has $s(a)E(t)$ on its diagonals. The matrix $F(t)$ is formed in a similar manner to represent the population dynamics.

In some parameterizations, it is assumed that a known vector is subtracted from the state vector either before or after the effect of F on the population. For example, the known vector might be the catch from the previous time period. The extension to the Kalman filter in this case is straightforward, an example of which can be found in Jazwinski (1970). Essentially, all predicted estimates of the state are corrected by the constant amount. The covariance and gain calculations are unaffected by the known vector.

The Kalman filter, Equations (14) through (21), assumes that the matrices F, B, G, H, R, Q, and Σ, and the vector μ are known. For fisheries problems, the matrices F and H usually depend on a set of parameters to be estimated (e.g., $F = mI$), and R, Q, and μ are to be estimated. Let θ be a vector containing the parameters that F and H depend on, and let $\Theta = (\theta, R, Q, \mu)$ be the total parameters of the model. Shumway and Stoffer (1982a) showed that conditional on Θ, the complete data likelihood is given by Equation (4). They apply a result of Dempster et al. (1977), which shows that maximum likelihood estimates of the parameters can be obtained by finding the conditional expectation (the E-step) of the complete data likelihood with respect to the missing "data" (in this case the missing data are the sufficient statistics of the normal distribution) and alternately estimating the expected value of the missing data, and then maximing the likelihood (the M-step) using the completed data. Shumway and Stoffer (1982a) showed that the expected conditional log-likelihood is given by Equations (6) through (8). All of the terms in this likelihood, for a given value of Θ, can be found by the Kalman filter. Moreover, given these values, the maximization problem is a deterministic one.

If we assume that the matrix F is independent of time and unrestricted, then Shumway and Stoffer (1982a) showed that the maximization step is accomplished by setting

$$F = S_t(1)S_{t-1}(0)^{-1} \tag{22}$$

$$Q = (S_t(0) - S_t(1)S_{t-1}^{-1}(0)S_t(1)^r)/T \tag{23}$$

$$R = T^{-1}\sum_{t=1}^{T}[(y(t) - H(t)x(t|T) \times (y(t) - H(t)x(t|T))^r + H(t)P(t|T)H(t)^r] \tag{24}$$

$$\mu = x(0|T). \tag{25}$$

where $$S_t(j) = \sum_{t=1}^{T}(P(t,t-j|T) + x(t|T)x(t-j|T)^r). \tag{26}$$

Shumway and Stoffer (1982a) gave a recursive formula for calculating $P(t, t-1|T)$ while performing the backward smoothing recursion.

If we assume that F is constrained to be of the form $F = \tilde{m}D$ where $\tilde{m}$ is a constant and D is a known matrix, then Shumway and Stoffer (1982b) showed that

$$Q = (C - \tilde{m}BD^{\tau} - \tilde{m}DB^{\tau} + \tilde{m}^2DAD^{\tau}) \quad (27)$$

$$\tilde{m} = \frac{tr(Q^{-1}BD^{\tau})}{tr(Q^{-1}DAD^{\tau})} . \quad (28)$$

Equations (27) and (28) can be solved by taking an initial guess for $\tilde{m}$, then iteratively solving for Q and $\tilde{m}$ until the values converge.

Finally, we can make explicit the effect of assuming equal variances and no covariances for both $w(t)$ and $v(t)$. For given estimates of Q and R, since both are square, symmetric matrices, they can be factored as

$$Q = U\,DU^{\tau}$$

$$R = LL^{\tau}$$

where U is an upper triangular matrix, D is a diagonal matrix, and L is the lower triangular square root of R. To obtain an underlying population dynamic that has an uncorrelated error vector $\tilde{w}(t)$ and uncorrelated observations with variances of 1, we make the following transformations:

$$\tilde{G} = GU$$

$$\tilde{y}(t) = L^{-1}y(t)$$

$$\tilde{H}(t) = L^{-1}H(t)$$

$$\tilde{v}(t) = L^{-1}v(t)$$

and replace G, w, y, H, and v in Equations (14) through (21) with the transformed values. Then $\tilde{v}(t)$ has covariance matrix I, and $\tilde{w}(t)$ has covariance matrix D. The assumption that both the error in the dynamics and in the observations are equal, further constrains the values of D to be identical. This is a very strong assumption.

AN EXAMPLE

As an example of these methods, I use the data for Pacific mackerel published in Parrish and MacCall (1978). I emphasize that I am only using these data for illustrative purposes and do not claim to be making a careful, thorough reexamination of the problem. Though $\tilde{m}$ can be estimated using Equation (28), I assume that the value of $\tilde{m}$ is known a priori. If I were to use a different value of $\tilde{m}$, it would be difficult to judge to what extent the new estimates differ solely due to the different mortality rate, rather than due to the estimation scheme. I assume, as in the reference, that the mortality rate m is equal to 0.5, so that the F matrix in my notation is a matrix with a value of 0.6065 in position $(i, i-1)$, $i = 2, \ldots, 7$, corresponding to the underlying dynamics for age groups 1 through 6.

Recruitment in Pacific mackerel is highly variable. I want to obtain estimates of recruitment that accurately reflect this variability while still being consistent with the observed data. Also, I do not want to a priori assume a functional relationship between recruitment and population size. To this end, I assume that the recruitment time series, after taking differences of a given order, is a random variable, i.e.,

$$\nabla^k r(t) = w(t) \quad (29)$$

where $w(t)$ is a normal random variable with a mean of zero and with an unknown variance σ^2 and ∇^k denotes kth order finite differencing. Akaike (1979) originally showed that this formulation is the discrete equivalent of fitting a spline to the data (in this case as a function of time), where the estimate of the variance σ^2 expresses the tradeoff between the degree of smoothness in the fitted curve with fidelity to the observed data. In this approach, k and the variance of $w(t)$ are treated as hyperparameters of the model. A fitting criterion such as AIC is then used to determine the best value of k given the data. Following Kitagawa and Gersch (1984), I could use smoothness priors to more generally decompose recruitment as

$$r(t) = T(t) + S(t) + \xi(t) + w(t) \quad (30)$$

where $T(t)$ is a trend term (as in Equation (29)), $S(t)$ is a seasonal term, and $\xi(t)$ is an irregular stationary term. A decomposition such as Equation (30) would be useful, for example, in modeling the monthly anchoveta recruitment considered in Mendelssohn and Mendo (1987). However, for convenience in this paper, I restrict recruitment to be of the form in Equation (29).

The relationship between this "smoothness priors" approach, "smoothing splines", and other penalized likelihood methods is discussed further for a variety of contexts in Brotherton and Gersch (1981), Kitagawa and Gersch (1984, 1985, 1988), Ansley and Kohn (1986), and Kohn and Ansley (1987, 1988). Wahba (1977) and O'Sullivan (1986) discussed the relationship between generalized cross-validation, penalized likelihood functions, and determining the tradeoff between smoothness and fit.

For $k = 0$, Equation (29) models recruitment as a random variable around a fixed but unknown mean value. For $k = 1$, Equation (29) models recruitment as a random walk with unknown mean level and drift (variance). Higher values of k have similar interpretations. Values of k higher than two or three rarely need to be considered, since these include the discrete equivalent of cubic splines. Cubic splines can approximate most functionals (in this case of time) to a reasonable degree of accuracy.

For this example, I assume $k = 1$, so that

$$r(t) = r(t - 1) + w(t) \tag{31}$$

which is a random walk with unknown variance. (A more complete analysis of this data would probably also include an irregular stationary term as in Equation (30) and determine the "best" order of differencing using a given criterion.) Equation (31) can be incorporated into the state space model by letting the (1,1) element of the matrix F be equal to 1. The matrices $H(t)$ are diagonal matrices whose values are calculated from table 13 in Parrish and MacCall (1978). Because I am assuming that the estimates of F are known, then the value of Q for the M step is maximized as

$$T^{-1}[S_t(0) - S_t(1)F^{\tau} - FS_t(1) + FS_{t-1}(0)F^{\tau}]. \tag{32}$$

As in Parrish and MacCall (1978), I treated age groups 4 through 6 as fully selected by the fishery, and will refer to these age groups as "adults". Similarly, I refer to the number of age-1 fish at the start of the season as the number of recruits. I assume that F and $H(t)$ are known, so the estimation problem is reduced to determining the means of the initial population sizes and the values of the two covariance matrices Q and R.

The resulting maximum likelihood estimates of Q and R (Tables 1, 2) show that the variances of the error terms differ by up to two orders of magnitude, hardly meeting the usual assumption of equal variances. Moreover, the covariances (expressed as correlations in the tables) are quite high, so that using $\frac{1}{\sigma}$ as a weighting factor will not be adequate. The predicted, filtered, and smoothed estimates of the adults (Fig. 1) are very similar, reflecting that the errors have been "filtered out" over time by the population dynamics.

TABLE 1.—Estimated values of the matrix Q presented as a variance-correlation matrix. The diagonal terms are the variances, and the off-diagonal terms are the cross-correlations.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	8.72E+09	−0.9075	0.2429	0.0592	0.1785	−0.2096	0.0249
Age 1		4.59E+09	−0.1750	−0.0574	−0.1658	0.1803	−0.0432
Age 2			1.07E+09	0.0396	0.2416	0.1109	0.0675
Age 3				5.28E+08	0.7030	0.5964	0.3140
Age 4					1.90E+08	0.6717	0.3944
Age 5						3.08E+07	0.4854
Age 6							2.18E+06

TABLE 2.—Estimated values of the matrix R presented as a variance-correlation matrix.

	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
Age 0	7.30E+07	−0.0497	0.8505	0.7367	0.6594	0.5120	−0.4019
Age 1		2.62E+07	0.1594	0.0896	−0.0544	−0.3411	0.4325
Age 2			4.95E+06	0.6764	0.6412	0.3830	−0.2418
Age 3				3.43E+06	0.7286	0.4908	−0.2260
Age 4					7.11E+05	0.5708	−0.2030
Age 5						2.05E+05	−0.1331
Age 6							5.40E+04

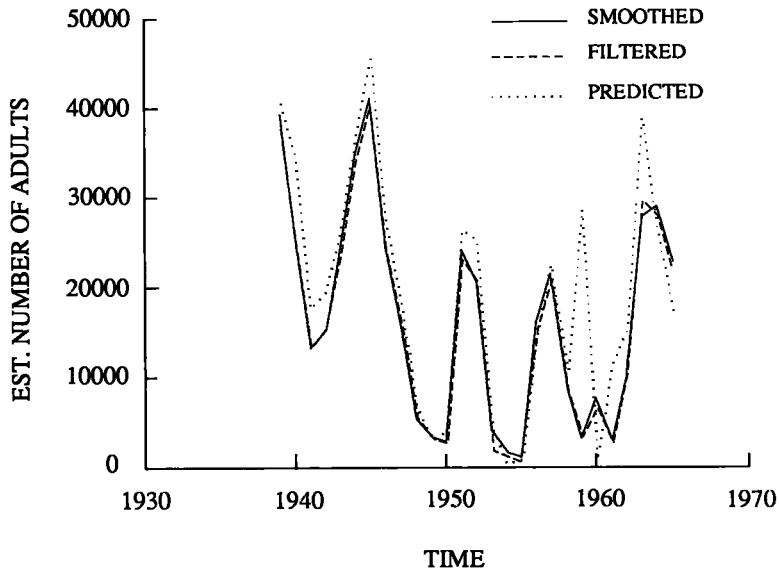

FIGURE 1.—Estimated number of adults, 1939–65, using values from Parrish and MacCall.

The predicted, filtered, and smoothed estimates of the recruits (Fig. 2), unlike those of the adults, are not similar. The filtered and smooth estimates are often indistinguishable, but there are some years (such as 1941 and 1943) where there are significant differences. The predicted values are very smooth, tending to emphasize the trend in the recruitment. In an analysis of recruitment estimates produced by standard cohort analysis of the anchoveta off Peru, Mendelssohn and Mendo (1987) found the estimates

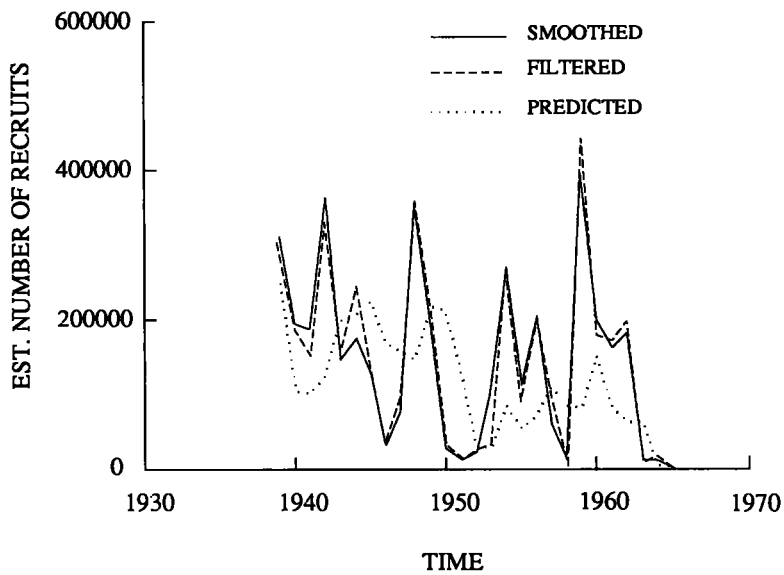

FIGURE 2.—Estimated number of recruits, 1939–65, using values from Parrish and MacCall.

to be far too smooth. The results of this present example may explain their observation. If these values were used in a subsequent analysis, say to determine the role of the environment on recruitment, a totally false picture of this relationship could emerge. I emphasize that the predicted estimates are calculated from the previous season's filtered values, whereas it is often true in the fisheries literature that the predicted values are estimated from the previous predicted values, rather than from the filtered values. Direct comparison with the estimate in Parrish and MacCall (1978) are difficult because restricting recruitment to be of the form (Equation (29)) with k fixed, rather than the more general form (Equation (30)) with k variable, may not be appropriate for the Pacific mackerel data. But overall, their estimates tend to resemble the smoother trend of my predicted estimates.

RELATIONSHIP TO OTHER LITERATURE AND A NEW PARAMETERIZATION

If the models are restricted to additive errors, then most of the simpler difference equation models proposed in Collie and Sissenwine (1983), Deriso et al. (1985), Fournier and Archibald (1982), Fournier and Doonan (1987), and among others can be formulated as I did. Some of these models assume recruitment is a nonlinear function of the underlying population, which cannot be handled in this model without some modifications (suggested below). However, all of these authors treat the underlying population sizes as parameters of the data rather than as missing data. As discussed earlier, it is questionable whether this will produce proper estimates of the underlying populations. Biases from treating missing data as parameters in a regression setting are explicitly discussed in Little and Rubin (1983, 1987).

A very broad class of possible models that can be selected to model catch-at-age data are given by Schnute (1985). He correctly identified the values that are parameters of the difference equations he discusses, and these are sufficient for estimating the likelihood (if evaluated properly). However, if we assume observation error, then it can be shown (see, for example, Shumway 1988) that the innovations are determined by predictors calculated from the previous period's filtered, rather than predicted values. Moreover, the minimum mean squared error estimates of the underlying populations, as discussed earlier, are the smoothed estimates. It appears that Schnute (1985) used the predicted or, at best, the filtered estimates of the underlying populations.

A popular parameterization that appears to have been first suggested by Doubleday (1976) is to assume that the observation matrix $H(t)$ is of the form $H(t) = \{s(a)f(t)\}$ where $s(a)$ is an age-dependent selectivity factor and $f(t)$ is a time-dependent exploitation rate. These values can be found by using a minimization routine during the M-step of the algorithm. However, it should be noted that the estimate of $f(t)$ for each t will depend on R and that the estimate of R will depend on both $s(\cdot)$ and $f(\cdot)$, so that either R, s, and f should be solved for together, or else they should be successively solved for using Equation (7) while holding the other parameter values fixed.

Alternatively, Equation (7) can be differentiated. Then for given values of $f(t)$, the optimum value of the vector $s(a)$ at each iteration are the diagonals of the matrix S given by

$$S = AB^{-1} \tag{33}$$

where $A = \sum_{t=1}^{T} y(t)x(t|T)^{\tau}f(t)$, and $B = \sum_{t=1}^{T} f^2(t)(P(t|T) + x(t|T)x(t|T)^{\tau}$. However, this is an unconstrained estimate and does not guarantee that $s(a)$ is between (0,1). It can be shown that the optimal solution is to set $s(a)$ at zero if $s(a)$ is negative or to 1 if $s(a)$ is greater than 1.

For fixed values of $s(a)$ and R, Equation (7) is maximized when $f(t)$ takes the value

$$f(t) = \frac{tr(R^{-1}y(t)x(t|T)^{\tau}S^{\tau})}{tr(R^{-1}S(P(t|T) + x(t|T)x(t|T)^{\tau})S^{\tau})} \tag{34}$$

where the matrix S is as above. This is the unconstrained solution. The constrained solution again is to force the estimate to lie within the closed interval (0, 1) as with the estimate of the $s(a)$. Since the estimates of R, $s(a)$, and $f(t)$ are interrelated, I have found it to be a workable procedure to first estimate Q as given above and then for a given number of iterations, iteratively solve for $f(t)$ then $s(a)$. When these values stabilize, estimate R using the formula given above. While this procedure does not necessarily maximize Equation (7), it is sufficient for the generalized EM algorithm the new values increase the function given in Equation (7).

As with the original estimates, the smoothed and filtered estimates of recruitment (Fig. 3) are close

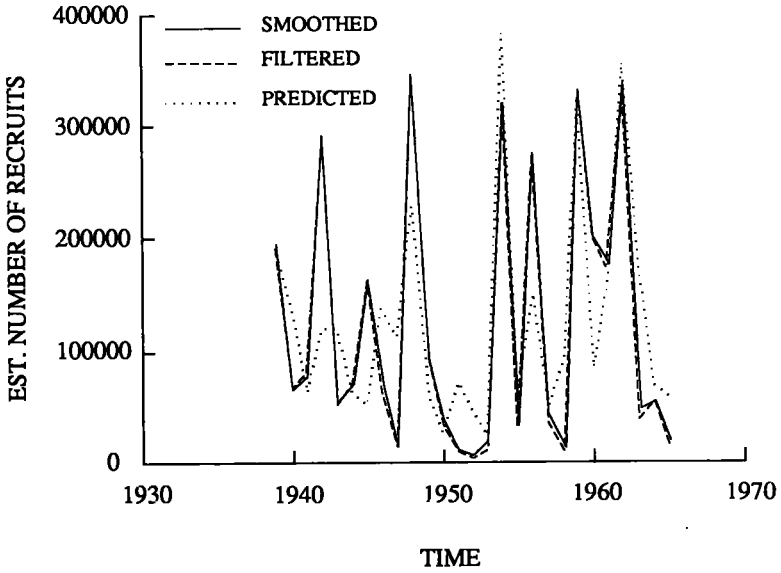

FIGURE 3.—Estimated number of recruits 1939–65, assuming $q(a, t) = f(t)s(a)$.

to each other, while the predicted values are too smooth. The estimated values of $f(t)$ (Fig. 4) generally decline with time. All three estimates are significantly different from the previous estimates. Years where relative highs and lows occur differ, showing the sensitivity of this class of models to the assumed form of the H matrix. Since the estimates of R, $s(a)$ and $f(t)$ are interrelated, I suspect that the parameter estimates are highly correlated and hence unstable. While I have not calculated the parameter covariance matrix, it should be checked for any serious analysis using these techniques.

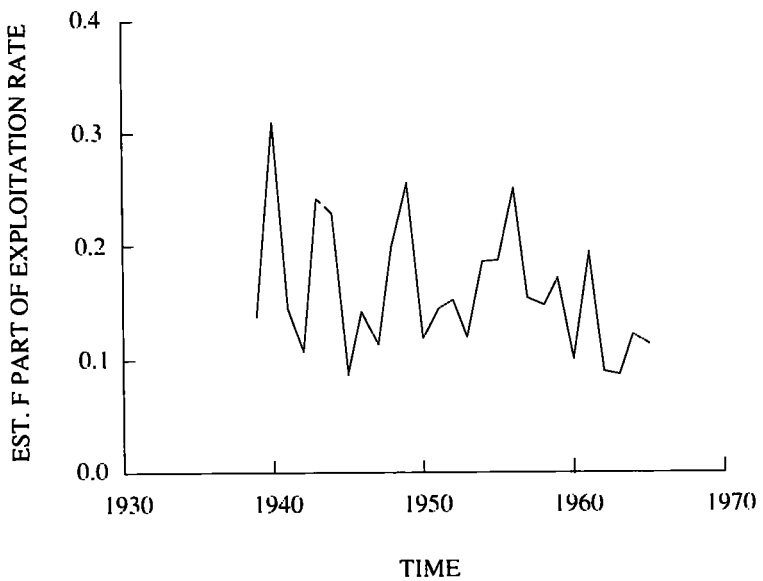

FIGURE 4.—Estimated values of $f(t)$ when $q(a, t) = f(t)s(a)$.

While the parameterization $H(t) = \{f(t)s(a)\}$ greatly reduces the number of parameters, I still face the same problem as when I treated the unobserved population as parameters: each new period adds another parameter to the model. The model still appears to be overparameterized, and the asymptotic theory for maximum likelihood estimation may be invalid.

As with the recruitment estimates, the number of effective parameters can be reduced by adding a smoothness prior on $f(t)$. However, $f(t)$ is a proportion and not likely to be a normal variable. The $f(t)$ are also constrained to lie in the interval $(0, 1)$, so a transformation to an unconstrained variable would also be desirable. If $f(t)$ is a binomial random variable then $\arcsin(\sqrt{f(t)})$ is approximately normal with nearly equal variance. This suggests the transformation of variables

$$f(t) = \sin^2(e(t)) \tag{35}$$

where $e(t)$ is an unconstrained normal variable. Then the smoothness prior becomes

$$\nabla^k e(t) = w(t) \tag{36}$$

(a smoothness prior that includes a seasonal component or irregular stationary part, as in Equation (30), can also be used), and for any age class, the observation equation becomes

$$y(a,t) = s(a)\sin^2(e(t))x(a,t). \tag{37}$$

The underlying population dynamics must also be expanded to include the smoothness prior constraint (Equation (36)).

Unfortunately, the observation equation is no longer linear in the state vector. The smoothness prior is a prior distribution on the $f(t)$, and a full Bayesian analysis can be done to obtain the overall distribution. The variance of $w(t)$ is then treated as a hyperparameter in the analysis.

A simpler approach is to evaluate the filter equations approximately by using any one of a number of nonlinear filters (see Anderson and Moore 1979). One that is easy to implement, given the nonlinearities in this problem, is the extended Kalman filter (EKF), which at each time period just linearizes all the nonlinear terms around the value of the predicted state vector. The EKF, however, can have divergence problems and is not guaranteed to find the true penalized likelihood estimates.

When using the EKF, it works to make a forward and backward pass of the filter given the current estimates of $f(t)$ and $x(t|T)$, and then to estimate $s(a)$ and R as before. I tested the algorithm on the mackerel data with $k = 1$ in the constraint (Equation (36)). The resulting estimates (Fig. 5) are similar to the previous estimates, but the estimated values of $f(t)$ (Fig. 6) are less variable with a stronger trend than before. It is clear from Figure 5 that the

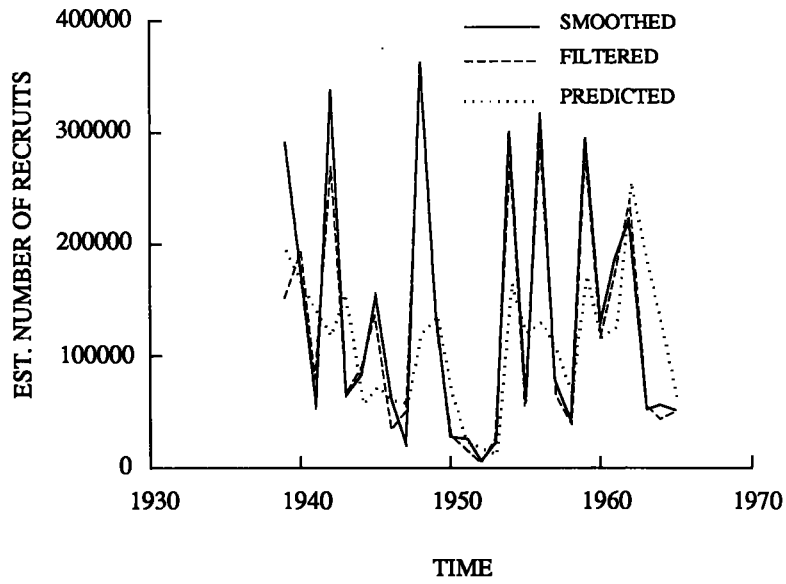

FIGURE 5.—Estimated number of recruits using a first order spline for estimating $f(t)$.

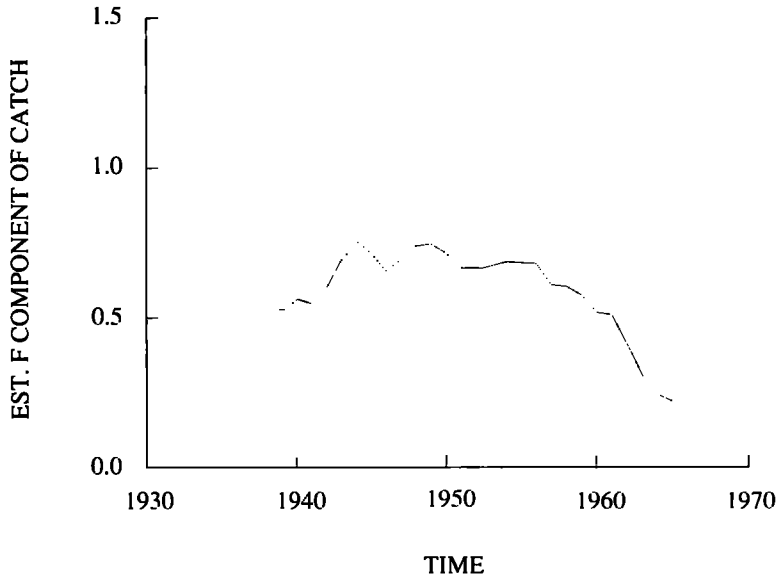

FIGURE 6.—Spline estimates of $f(t)$.

smoothness prior estimate has shifted some of the variation in the observed data to variations in the underlying population dynamics rather than variations in $f(t)$. Further research needs to be done to see which of these estimates is the most "valid".

The EM algorithm in general can be sensitive to the initial values given the parameters (see Wu 1983), and I have found that the fixed value of Σ can also affect the estimates. Initial combinations of μ, $f(t)$, and $s(a)$ that are totally inconsistent with the observed catch data can cause the algorithm to find a local maximum. This can be avoided by experimenting with several, very different starting values and determining if they converge to the same estimates.

If recruitment is thought to be a linear function of the previous population size, then there is no problem including this in the Kalman filter. If recruitment is a nonlinear function of the previous population, then the EKF can again be used to approximately determine the conditional expectations needed for the EM algorithm.

If information is available from a variety of sources, say from fishing and from surveys, as in Methot (fn. 2), then each of the vectors and matrices can be partitioned to represent this situation. For example, let $y_s(t)$ be the observed catches from a survey and $y_f(t)$ the observed catches from fishing. Let $y(t)^T = (y_s(t), y_f(t))^T$, and partition the H matrix similarly. Then the diagonal blocks of H will contain the observation dynamics for the survey and for fishing, while the off-diagonal blocks will be zero. Given these modifications, all the algorithms described previously in this paper can be used to derive estimates for this situation.

Research or other surveys of the fishery usually occur less frequently than does commercial fishing, causing part of the vector $y(t)$ to be missing at given times periods. Shumway and Stoffer (1982a) and Shumway (1988) gave a straightforward modification of the Kalman filter for this case.

DISCUSSION

I have introduced a new method for estimating population sizes from catch-at-age data that includes, if additive errors can be assumed, many of the previous difference equation models. I show that it is incorrect to treat the unobserved population sizes as parameters to be estimated rather than as missing data. I also show that the minimum mean square estimates of the population sizes are the smoothed estimates rather than the predicted estimates suggested in many papers. The model assumes neither equal variances in the errors in the population dynamics nor in the observation errors and does not require that the errors be uncorrelated. For Pacific mackerel, the smoothed estimates are shown to be much more variable than the predicted estimates.

I also suggest a new parameterization for the age-specific exploitation rate $q(a,t)$. If it is assumed that $q(a,t) = s(a)f(t)$, then the model is over determined. I put a smoothness prior on $f(t)$ in order to obtain a tradeoff between the degree of smoothness in $f(t)$ as a function of time versus fidelity to the data. The degree of differencing can be treated as a hyperparameter of the model to determine the optimal amount of differencing given the data.

An advantage of the approach of this paper is that the calculations are straightforward and simple to program, and explicit formulas are given for the optimal parameter values at each iteration of the EM algorithm. Additional optimization software is not required to perform the calculations. Moreover, properties of the Kalman filter and the EM algorithm are well known. There is a large literature giving variants of the filter to calculate sensitivity to model misspecification, and recursive formulas for the derivatives with respect to a given parameter of the model also exist in the literature.

It is also simple to include environmental variables into the formulation, either as additional state variables or as fixed effects in the observation equation or both (see Sallas and Harville [1988] on how to estimate the fixed effect parameters within the context of Kalman filtering). Thus the influence of the environment can be modeled directly, rather than resorting to the conventional practice of obtaining population estimates first and correlating these estimates with the environmental variables second.

A disadvantage of my approach is that there is no guarantee that any of the estimates of the underlying population sizes will be positive. The population sizes are treated as normal random variables, and it is quite possible for the additive corrections in the filtered or smoothed estimates to make small population sizes negative if the observation error is large. P. Sullivan (fn. 3) has found that for a length-based model the Kalman filtering approach works best when there are pulses in the recruitment, that is, when the population is not in equilibrium. The likelihood surface is such that without recruitment pulses it is difficult to estimate the parameters of the growth-curve. Most fisheries are not in equilibrium, however. As the models in this paper do not contain a growth-curve, it is unclear if a similar finding will be valid.

Some of my results suggest that the estimates are sensitive to the form of the model chosen for the population dynamics. This is not surprising, because, unlike most missing data problems, the missing part of the data is never observed directly, but only through the presumed form of the dynamics. For example, when modeling catch (or catch per unit effort) against an environmental variable, catch data often are not available for all periods. But there are at least some periods when both variables are observed, which can be used to estimate the relationship between the two sets of variables. This relationship is used to produce the smoothed estimates of the missing data. For estimating population sizes from catch-at-age data, the a priori estimate of the form of the observation equation replaces this empirically derived estimate.

In many of the references cited, multiplicative errors are preferred in the observation equation because variances appear to change with the size of the population. My experience is that relaxing the assumption of equal, uncorrelated errors appears to at least partially take into account the observed differences. If the model estimates are not satisfactory, assuming additive, gaussian errors, then the regular EM algorithm can be used to properly estimate the smoothed estimates of the underlying population. However, the EM algorithm requires the complete data likelihood as well as the expectation of the log-likelihood with respect to $(y(1), \ldots, y(T))$. In multiplicative models, assumptions about the error structure can lead to very complicated multivariate distributions for the complete data due to the Jacobian of the transformation. The conditional expectation of the log-likelihood may have to be evaluated by numerically integrating a nontrivial multiple integral. Certainly, as a first pass, the simpler techniques of this paper would appear to have a lot to offer as an alternative.

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INTEGRITY OF SCHOOLS OF SKIPJACK TUNA, *KATSUWONUS PELAMIS*, IN THE EASTERN PACIFIC OCEAN, AS DETERMINED FROM TAGGING DATA

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ABSTRACT

Little information concerning the integrity of schools is available for any species of fish. In this study the integrity of schools of skipjack tuna, *Katsuwonus pelamis*, was analyzed with data for returns of tagged fish which had been in the same schools when originally tagged. Two methods, the first using Chi-square contingency tests and the second using binomial homogeneity tests, were employed. From the results obtained with the first method it appears that after 1 month at liberty the tagged and untagged fish were randomly mixed with one another in some cases and after 3 to 5 months at liberty they were randomly mixed with one another in nearly all cases. The results obtained with the second method indicate somewhat less rapid mixing of the tagged and untagged fish.

Schooling occurs in many species of fish, and many studies have been made of the reasons for schooling and the behavior of the fish in the schools (e.g., Parr 1927; Shaw 1970; Pitcher 1986). Almost nothing has been written, however, about the integrity of schools over extended periods of time.

Parr (1927) stated that "apparently permanent" schools are formed by pelagic fishes such as mackerel, sprat, and herring, and Sharp (1978) reported that, "From the genetic sample data for the eastern Pacific yellowfin [(*Thunnus albacares*)] and the Pacific-wide skipjack [(*Katsuwonus pelamis*)] there is evidence for a cohesiveness of related fishes in schools.... What is observed is that where more than one very rare allele (overall expected occurrence <.01) is encountered in a large sample, the individuals exhibiting the rare alleles are often the same length or within 1 cm of each other. This is highly unlikely unless they are related."

On the other hand, Helfman (1981) reported "aggregations [of freshwater fish] that disbanded during twilight," and Moyle and Cech (1982) stated that "most schools break up at night." Observers on fishing vessels and aircraft have reported that the schools of tunas frequently break up and reform. Scott and Flittner (1972), for example, stated that "the relatively large nighttime schools [of bluefin tuna, *Thunnus thynnus*,] break down into several smaller foraging schools and begin their search for food.... The gradual increase in school size during the daylight hours may be due to regrouping of the smaller schools through random encounters." Such observations might lead to the conclusion that there is considerable mixing of fish from different schools and that fish of the same species and same approximate size in the same areas would mix thoroughly with one another within a period of a few days or weeks.

Anonymous (1960) stated that "Tag returns from individual schools [of skipjack tuna] suggest that, normally, the skipjack in Hawaiian waters remain within a school for one month or less, then at least some of the school break off, move into new areas, and regroup with other fish or schools. From the releases off Hilo and Mexico, however, it is evident that there are situations, possibly environmentally conditioned, where the schools remain intact...for at least 2 or 3 months." Lester et al. (1985) studied the occurrence of various parasites in skipjack tuna of the same and different schools and concluded that "school half-life is likely to be in terms of at least weeks rather than days." They stated, however, that their data did "not support the hypothesis [of Sharp (1978)] that fish stay in the same school for life."

Examination of data for fish tagged and released at the same location and time shows that some have been recaptured weeks or months later in the same purse seine set or baitboat stop, and others have been recaptured weeks or months later on the same date in widely separated locations (Hunter et al.

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1986). (Henceforth in this report, to save space, both sets and stops will be referred to as sets.) The former results might be due merely to chance. The latter results indicate that not all the fish remain together at all times, but this information is of limited value. A much more powerful method of analysis is needed. Turner (1986) employed statistical tests to show that tagged bluefin tuna caught during the calendar year after release had mixed considerably with the untagged population, but knowledge about shorter term mixing is necessary for short-lived species, such as skipjack tuna. The present report describes what are believed to be new and useful methods of analysis of the integrity of schools of fishes, using data for tagged skipjack tuna released and recaptured in the eastern Pacific Ocean.

MATERIALS AND METHODS

The methods of tagging the fish are described by Bayliff and Holland (1986).

Tagged fish, or tags unaccompanied by the fish to which they were attached, are recovered and returned by fishermen, unloaders, and cannery workers, accompanied by information which is used to assign them to specific sets. Additional details regarding this aspect of the study are discussed later in this report.

The methods of collecting and processing the catch statistics are discussed by Shimada and Schaefer (1956) and Joseph and Calkins (1969). Hennemuth (1957) and Shingu et al. (1974) described the methods of sampling the fish and the calculations employed to determine the size composition of tunas in the catches. The areas shown in Hennemuth's figure 1 have been changed several times since that report was published, however; the areas used currently are shown by Peterson (1982: fig. 30).

ANALYSES AND RESULTS

If tagged fish released at the same location on the same day mix thoroughly with the population of untagged fish in the same area, schools of fish caught in that area will have approximately equal ratios of tagged to total fish, whereas if they do not mix thoroughly some of the schools will have much higher ratios than the others. In this report the numbers of tagged fish recaptured in sets made at various intervals after release are compared with the numbers of tagged fish which would be expected in those sets if the tagged fish had mixed thoroughly with the rest of the population during the interval

TABLE 1.—Data used for analysis of integrity of schools of skipjack tuna. The ranges of values of sets and average weight in pounds are explained in the text.

Tagging cruise	Dates of release	Month of recapture	Numbers of returns	Sets	Average weight in pounds
1042	2, 3, 4, 17, 18, 19, 23, 24 June 1962	June	439	60–228	5.86–6.84
		July	152	174	5.85
		August	44	333	4.96
1043	5, 9, 20, 27, 28 June; 1 July 1963	June	130	11–89	6.10–6.27
		July	248	265–282	6.08–6.10
		August	108	385	5.74
		September	39	388	6.99
		October	13	247	4.98
1070	12, 13, 14, 30 June 1973	June	7	118–129	5.21–5.22
		July	32	144	5.08
		August	15	120	4.59
		September	27	45	5.35
		October	33	205	5.26
		November	10	229	5.69
1075	26 June; 20, 21 (two releases) July 1975	July	13	42–215	5.56–6.12
		August	55	274	6.83
1079	9, 10, 17, 18, 19 June 1976	June	158	232–297	4.31–4.32
		July	261	386	4.29
		August	15	47	4.24
		September	118	542	4.88
		October	61	546	4.56
		November	6	262	4.12

between release and recapture. A description of how this was done is given below. The data used in the analyses are summarized in Table 1, and a more detailed summary of the data for tagging cruise 1079, which will be discussed in more detail than the other cruises, is given in Table 2.

First, the units of time to be employed were selected. Tagged skipjack tuna have been recaptured after as long as 3 years at liberty, but the great majority of recaptures have been made within 6 months after release. It was decided to examine the data by monthly intervals because, for the experiments with sufficient total numbers of returns, that would produce several intervals with sufficient numbers of returns of tagged fish for each interval. Also, the statistical and size-frequency data of the Inter-American Tropical Tuna Commission (IATTC) are routinely calculated by month (and quarter and year), so no special calculations are required.

TABLE 2.—Data from cruise 1079 used for analysis of integrity of schools of skipjack tuna.

Date of release	Month of recapture	Numbers of returns	Sets	Average weight in pounds
9 June 1976	June	13	297	4.32
	July	13	386	4.29
	August	1	47	4.24
	September	5	542	4.88
	October	3	546	4.56
	November	0	262	4.12
10 June 1976	June	26	294	4.32
	July	17	386	4.29
	August	0	47	4.24
	September	8	542	4.88
	October	5	546	4.56
	November	1	262	4.12
17 June 1976	June	80	252	4.32
	July	120	386	4.29
	August	9	47	4.24
	September	48	542	4.88
	October	31	546	4.56
	November	1	262	4.12
18 June 1976	June	33	240	4.32
	July	88	386	4.29
	August	4	47	4.24
	September	43	542	4.88
	October	18	546	4.56
	November	2	262	4.12
19 June 1976	June	6	232	4.31
	July	23	386	4.29
	August	1	47	4.24
	September	14	542	4.88
	October	4	546	4.56
	November	2	262	4.12
Total	June	158	297	4.32
	July	261	386	4.29
	August	15	47	4.24
	September	118	542	4.88
	October	61	546	4.56
	November	6	262	4.12

Second, the areas of study were selected. If the tagged fish are released at a particular location, the vessels fishing near that location would catch more tagged fish, at least during the first few months after release, than would vessels fishing several hundred or more miles away. Thus only data for the vessels fishing near the location of release should be considered. The areas of study were selected by examining charts of the distributions of fishing effort and recaptures of tagged fish, by 1-degree areas and by months, and arbitrarily excluding those with lower recaptures per unit of fishing effort. This was quite simple, as during the periods in question practically no tagged fish were recaptured south of lat. 20°N, and there was little fishing effort north of lat. 20°N outside the area-time strata selected. The areas of study for the data for tagging cruise 1079 are shown in Figure 1.

Third, a list of sets for each area-time stratum was prepared. This included the weights of skipjack tuna caught (Table 3, column 2) and the numbers of tagged fish returned (Table 3, column 4). (Throughout this report the weights are expressed in short tons [0.907 metric tons] and pounds [0.454 kg]. The IATTC uses this system because the fishermen estimate the weights of the fish caught in individual sets in short tons, and these estimates are an important component of its data base.) In a few cases the catches were recorded only as weights of mixed skipjack tuna and some other species, and in those cases the weights were divided by 2, assuming that they consisted of equal weights of skipjack tuna and the other species. (The rest of this table will be discussed later.)

It can be seen in Table 1 that ranges instead of individual values are given for "Sets" for cases when the month of recapture is the same as the month of release. This is because sets made before the date of release were not considered for the analyses, and it was also decided not to use data for tagged fish recaptured on the date of release because these could not have mixed with the rest of the fish in the area to any appreciable extent. Therefore for cruise 1079, for example, there were 297 June sets after 9 June, 294 after 10 June, 252 after 17 June, 240 after 18 June, and 232 after 19 June (Table 2).

Fourth, an average weight for each month of recapture for each experiment was selected. Monthly average weight data for purse seine- and baitboat-caught fish from area 1 in Peterson (1982: fig. 30) were used for this purpose because they closely correspond to the strata selected for study. The aver-

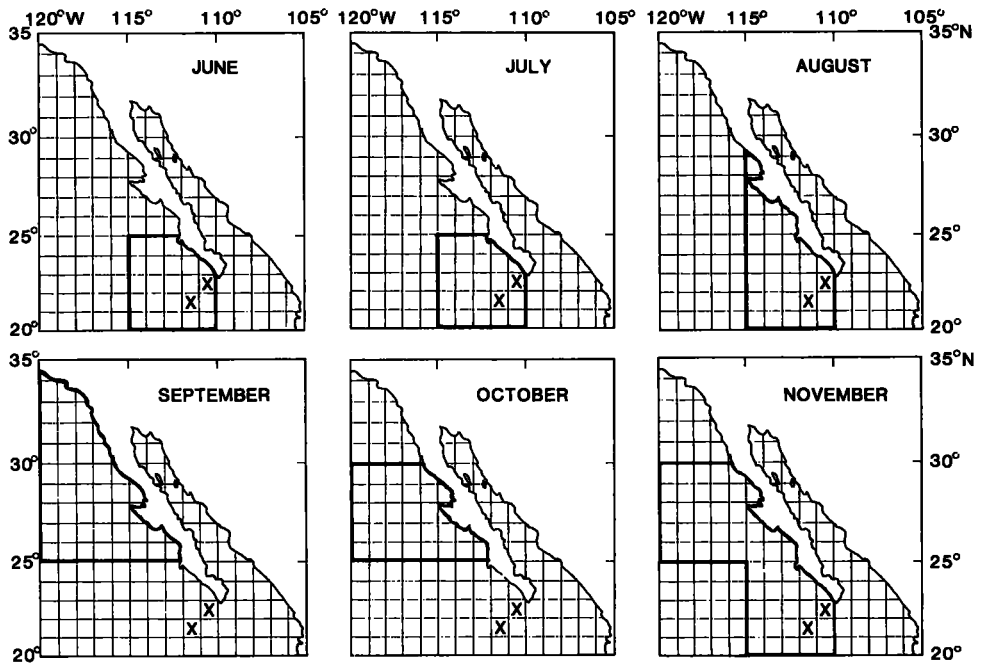

FIGURE 1.—Locations of release (X's) and areas of recapture selected for tagging cruise 1079 (areas delineated by heavy lines).

age weights were estimated by

$$\bar{w}_j = \frac{\left(\sum_{i=1}^{n} W_{ijPS} \times \bar{w}_{jPS}\right) + \left(\sum_{i=1}^{n} W_{ijBB} \times \bar{w}_{jBB}\right)}{\sum_{i=1}^{n} W_{ijPS} + \sum_{i=1}^{n} W_{ijBB}}$$

where $\bar{w}_j$ = average weight of skipjack tuna in stratum j,

W_{ijPS} and W_{ijBB} = weights of skipjack tuna caught in purse seine set i and baitboat set i, respectively, made in stratum j,

n = number of purse seine or baitboat sets in stratum j, and

$\bar{w}_{jPS}$ and $\bar{w}_{jBB}$ = average weights of skipjack tuna caught in stratum j by purse seiners and baitboats, respectively.

These are listed in Tables 1 and 2.

The average weights usually differ within strata which correspond to the months of release (Tables 1, 2) because only the sets after the dates of release are considered, and the portions of the total catches which are from purse seines and baitboats differ in accordance with the dates considered.

The data were analyzed by 1) Chi-square contingency tests and 2) the binomial homogeneity test described by Kendall and Stuart (1961:578–579).

Chi-Square Contingency Tests

A computer program, SCHOOL, was written to analyze the data. For a given release date and month of recapture, this program estimates the number of fish caught in each set from the weight of fish caught and the average weight of the fish. It then sums the estimates of the numbers of fish caught and numbers of tagged fish returned for all sets and calculates the tagged to total ratio. This ratio is then used with the equation for the binomial distribution to estimate the probabilities of 0, 1, 2, 3,. . . tagged fish appearing in each set if the fish are randomly mixed. The sums of the probabilities for all the sets for 0, 1, 2, 3,. . . tagged fish are then calculated so that these can be compared with the observed data, as described in the next paragraph. A sample output

from this program is shown in Table 3. It can be seen that the sum of 39.40 + 6.41 + 1.00 + 0.16 + 0.02 (last line) is equal to 47, the number of sets, and that the sum of (39.40 × 0) + (6.41 × 1) + (1.00 × 2) + (0.16 × 3) is equal to 9, the number of tagged fish returned. (The numbers of tagged fish returned for each set had been entered in Table 3, column 4, as explained above. If the total, 9, had been entered for the first set, or any other set, however, the result in the bottom line would have been the same.)

The bottom lines from all the outputs from SCHOOL for tagging cruise 1079 are listed in the "exp." (expected) lines of Table 4. Just below these are listed the observed ("obs.") numbers of sets with 0, 1, 2, 3,. . . tagged fish. At the bottom of each section of this table the sums of the expected and observed values are listed. Chi-square tests were run, using MINITAB (Ryan et al. 1985), on the expected

TABLE 3.—Probabilities of 0, 1, 2, 3,. . . 10 tagged fish in sets made in August in the area shown in Figure 1 from fish released on 17 June 1976. This table is similar to the output from program SCHOOL except that (1) normally the lines for the individual sets are not printed and (2) the output does not include the numbers of fish.

			Tags											
Set	Tons	Fish		*P*(0)	*P*(1)	*P*(2)	*P*(3)	*P*(4)	*P*(5)	*P*(6)	*P*(7)	*P*(8)	*P*(9)	*P*(10)	Total
1	12.0	5,660	0	0.6921	0.2546	0.0468	0.0057	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
2	15.5	7,311	1	0.6217	0.2954	0.0702	0.0111	0.0013	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
3	15.0	7,075	0	0.6313	0.2903	0.0667	0.0102	0.0012	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
4	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
5	3.0	1,415	0	0.9121	0.0838	0.0038	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
6	1.0	472	1	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
7	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
8	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
9	25.0	11,792	0	0.4646	0.3561	0.1365	0.0349	0.0067	0.0010	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
10	25.0	11,792	0	0.4646	0.3561	0.1365	0.0349	0.0067	0.0010	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
11	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
12	1.0	472	3	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
13	1.0	472	0	0.9698	0.0296	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
14	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
15	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
16	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
17	9.0	4,245	0	0.7588	0.2093	0.0289	0.0027	0.0002	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
18	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
19	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
20	22.0	10,377	1	0.5093	0.3436	0.1159	0.0260	0.0044	0.0006	0.0001	0.0000	0.0000	0.0000	0.0000	0.9998
21	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
22	1.5	708	0	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
23	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
24	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
25	8.0	3,774	0	0.7824	0.1919	0.0235	0.0019	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
26	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
27	13.0	6,132	0	0.6712	0.2675	0.0533	0.0071	0.0007	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
28	4.5	2,123	0	0.8711	0.1201	0.0083	0.0004	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
29	6.0	2,830	0	0.8319	0.1530	0.0141	0.0009	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
30	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
31	3.0	1,415	0	0.9121	0.0838	0.0038	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
32	6.5	3,066	0	0.8193	0.1632	0.0162	0.0011	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
33	7.0	3,302	0	0.8068	0.1731	0.0186	0.0013	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
34	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
35	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
36	1.5	708	1	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
37	1.5	708	0	0.9550	0.0438	0.0010	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
38	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
39	4.0	1,887	0	0.8846	0.1084	0.0066	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
40	10.0	4,717	0	0.7359	0.2256	0.0346	0.0035	0.0003	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
41	8.0	3,774	0	0.7824	0.1919	0.0235	0.0019	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
42	5.0	2,358	0	0.8578	0.1314	0.0101	0.0005	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
43	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
44	2.5	1,179	0	0.9262	0.0709	0.0027	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
45	7.5	3,538	2	0.7945	0.1827	0.0210	0.0016	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
46	2.0	943	0	0.9405	0.0575	0.0018	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9998
47	0.5	236	0	0.9848	0.0150	0.0001	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000	0.9999
Total	293.5	138,443	9	39.40	6.41	1.00	0.16	0.02	0.00	0.00	0.00	0.00	0.00	0.00	46.99

TABLE 4.—Data for analysis, by Chi-square contingency tests, of the integrity of schools of skipjack tuna released during tagging cruise 1079. [exp. = expected; obs. = observed.]

Date of release	Month of recapture	Tags		Occurrences of tagged fish 0	1	2	3	4	5	>5	Total	χ^2 value	df	Probability
9 June	June	13	exp.	284.87	11.38	0.63	0.09	0.02			297.00	0.001	1	>0.05
1976		13	obs.	285	11	1					297			
10 June		26	exp.	271.06	20.61	1.81	0.32	0.11	0.04	0.01	294.00	4.672	1	<0.05
1976		26	obs.	281	8	2	1		1	1	294			
17 June		80	exp.	194.53	44.10	9.32	2.23	0.68	0.31	0.76	252.00	16.032	2	<0.01
1976		80	obs.	218	20	6	4			4	252			
18 June		33	exp.	212.49	23.70	2.82	0.56	0.22	0.11	0.08	240.00	2.316	1	>0.05
1976		33	obs.	220	13	3	2	2			240			
19 June		6	exp.	226.26	5.50	0.21	0.02				232.00	0.012	1	>0.05
1976		6	obs.	226	6						232			
Total		158	exp.	1,189.21	105.29	14.79	3.22	1.03	0.46	0.85	1,315.00	38.280	3	<0.01
		158	obs.	1,230	58	12	7	2	1	5	1,315			
9 June	July	13	exp.	373.43	12.14	0.40	0.01				386.00	0.203	1	>0.05
1976		13	obs.	375	9	2					386			
10 June		17	exp.	369.73	15.56	0.66	0.03				386.00	0.686	1	>0.05
1976		17	obs.	373	10	2	1				386			
17 June		120	exp.	294.44	70.30	15.83	3.93	1.05	0.28	0.09	386.00	80.519	3	<0.01
1976		120	obs.	339	20	8	8	5	4	2	386			
18 June		88	exp.	314.41	58.43	10.48	2.08	0.43	0.09	0.02	386.00	31.073	2	<0.01
1976		88	obs.	342	22	9	8	2	2	1	386			
19 June		23	exp.	364.32	20.43	1.16	0.07				386.00	0.662	1	>0.05
1976		23	obs.	368	14	3	1				386			
Total		261	exp.	1,716.33	176.86	28.53	6.12	1.48	0.37	0.11	1,930.00	141.566	3	<0.01
		261	obs.	1,797	75	24	18	7	6	3	1,930			
9 June	August	1	exp.	46.02	0.96	0.02					47.00			
1976		1	obs.	46	1						47			
10 June		0	exp.	47.00							47.00			
1976		0	obs.	47							47			
17June		9	exp.	39.40	6.41	1.00	0.16	0.02			47.00	0.402	1	>0.05
1976		9	obs.	41	4	1	1				47			
18 June		4	exp.	43.30	3.42	0.26	0.02				47.00			
1976		4	obs.	44	2	1					47			
19 June		1	exp.	46.02	0.96	0.02					47.00			
1976		1	obs.	46	1						47			
Total		15	exp.	221.74	11.75	1.30	0.18	0.02			235.00	0.408	1	>0.05
		15	exp.	224	8	2	1				235			

and observed values, and the results are shown in the last four columns of Table 4. The categories were combined so that none had an expected value of less than 5. For the first test in Table 4 (releases on 9 June 1976, and recaptures during June), for example, the expected values are 284.87 and (11.38 + 0.63 + 0.09 + 0.02 = 12.12) and the observed values are 285 and (11 + 1 = 12). When only one category had an expected value of 5 or greater no test was run.

The two total lines for each section of Table 4 are listed in Table 5, with the equivalent values for the other four experiments. These were summed for each cruise and month of recapture, and Chi-square tests were run with these sums. Those results are shown in the last four columns of Table 5.

The results of the tests are summarized as follows:

		Months of recapture					
Category	*df*	*6*	*7*	*8*	*9*	*10*	*11*
releases made on	1	3/11	2/17	0/12	0/10	0/6	
individual dates	2	1/1	3/4	0/1			
	3	1/1	2/2				
	4	2/2					
totals for cruises	1	0/1	0/2	0/4	0/2	0/3	0/2
	2		1/1	0/1	1/1		
	3	1/2	2/2				
	4	1/1					
overall totals	1					0/1	0/1
	2			1/1	1/1		
	3		1/1				
	4	1/1					

TABLE 4.—*Continued.*

Date of release	Month of recapture	Tags		Occurrences of tagged fish 0	1	2	3	4	5	>5	Total	χ^2 value	df	Probability
9 June 1976	September	5	exp.	537.05	4.90	0.05					542.00			
		5	obs.	537	5						542			
10 June 1976		8	exp.	534.12	7.75	0.12					542.00	0.002	1	>0.05
		8	obs.	534	8						542			
17 June 1976		48	exp.	498.05	40.23	3.35	0.30	0.03			542.00	2.969	1	>0.05
		48	obs.	509	20	12		1			542			
18 June 1976		43	exp.	502.28	36.68	2.77	0.22	0.02			542.00	0.889	1	>0.05
		43	obs.	508	26	7	1				542			
19 June 1976		14	exp.	528.37	13.26	0.35	0.01				542.00	0.030	1	>0.05
		14	obs.	529	12	1					542			
Total		118	exp.	2,599.87	102.82	6.64	0.53	0.05			2,710.00	39.481	2	<0.01
		118	obs.	2,617	71	20	1	1			2,710			
9 June 1976	October	3	exp.	543.02	2.96	0.02					546.00			
		3	obs.	544	1	1					546			
10 June 1976		5	exp.	541.06	4.88	0.06					546.00			
		5	obs.	541	5						546			
17 June 1976		31	exp.	517.04	27.07	1.74	0.13	0.01			546.00	1.766	1	>0.05
		31	obs.	524	15	5	2				546			
18 June 1976		18	exp.	528.71	16.60	0.65	0.03				546.00	0.099	1	>0.05
		18	obs.	530	14	2					546			
19 June 1976		4	exp.	542.04	3.93	0.04					546.00			
		4	obs.	542	4						546			
Total		61	exp.	2,671.87	55.44	2.51	0.16	0.01			2,730.00	1.465	1	>0.05
		61	obs.	2,681	39	8	2				2,730			
9 June 1976	November	0	exp.	262.00							262.00			
		0	obs.	262							262			
10 June 1976		1	exp.	261.00	0.99						262.00			
		1	obs.	261	1						262			
17 June 1976		1	exp.	261.00	0.99						262.00			
		1	obs.	261	1						262			
18 June 1976		2	exp.	260.02	1.96	0.02					262.00			
		2	obs.	260	2						262			
19 June 1976		2	exp.	260.02	1.96	0.02					262.00			
		2	obs.	260	2						262			
Total		6	exp.	1,304.04	5.90	0.04					1,310.00	0.000	1	>0.05
		6	obs.	1,304	6						1,310			

This means that for individual dates for recaptures during June (i.e., during the month of release), 3 of 11 tests equivalent to those in Table 4 with 1 degree of freedom were significant at the 5% level; for recaptures during July, 2 of 17 tests equivalent to those in Table 4 with 1 degree of freedom were significant; and so on. From these tests it appears that after 1 month at liberty the tagged and untagged fish are randomly mixed with one another in some cases, and after 3 to 5 months at liberty they are randomly mixed with one another in nearly all cases.

Binomial Homogeneity Tests

For the binomial homogeneity test the formula

$$\chi^2 = \sum_{i=1}^{n} \frac{(T_i - F_i\hat{P})^2}{F_i\hat{P}(1 - \hat{P})}$$

where T_i = number of tagged fish in set i,
F_i = number of tagged and untagged fish in set i,
n = number of sets, and
$\hat{P}$ = probability of a fish being tagged = $\sum_{i=1}^{n} (T_i) / \sum_{i=1}^{n} (F_i)$

is used. Computer program SCHOOLA was used for this purpose.

The results are given in Table 6. In general, the

TABLE 5.—Data for analysis, by Chi-square contingency tests, of the integrity of schools of skipjack tuna released during all cruises. [exp. = expected; obs. = observed.]

Tagging cruise	Month of recapture	Tags		Occurrences of tagged fish								χ^2 value	df	Probability
				0	1	2	3	4	5	>5	Total			
1042	June	439	exp.	971.84	193.13	53.10	19.75	8.53	3.89	4.76	1,255.00	121.553	4	<0.01
		439	obs.	1,114	74	26	11	4	7	19	1,255			
1043		130	exp.	203.70	39.03	11.32	4.42	2.08	1.16	4.29	266.00	5.428	3	>0.05
		130	obs.	212	27	11	8	3	3	2	266			
1070		7	exp.	345.25	6.51	0.23	0.01				352.00	0.009	1	>0.05
		7	obs.	345	7						352			
1079		158	exp.	1,189.21	105.29	14.79	3.22	1.03	0.46	0.85	1,315.00	38.280	3	<0.01
		158	obs.	1,230	58	12	7	2	1	5	1,315			
Total		734	exp.	2,710.00	343.96	79.44	27.40	11.64	5.51	9.90	3,188.00	149.523	6	<0.01
		734	obs.	2,901	166	49	26	9	11	26	3,188			
1042	July	152	exp.	1,265.04	107.21	15.36	3.20	0.75	0.17	0.27	1,392.00	32.137	2	<0.01
		152	obs.	1,307	55	22	4	0	1	3	1,392			
1043		248	exp.	1,479.32	158.72	26.60	6.72	2.19	0.79	0.44	1,675.00	50.425	3	<0.01
		248	obs.	1,536	96	18	12	6	2	5	1,675			
1070		32	exp.	545.75	28.57	1.54	0.09				576.00	0.002	1	>0.05
		32	obs.	546	28	2					576			
1075		13	exp.	338.04	11.01	0.84	0.09				350.00	2.130	1	>0.05
		13	obs.	343	6					1	350			
1079		261	exp.	1,716.33	176.86	28.53	6.12	1.48	0.37	0.11	1,930.00	141.566	3	<0.01
		261	obs.	1,797	75	24	18	7	6	3	1,930			
Total		706	exp.	5,344.48	482.37	72.87	16.22	4.42	1.33	0.82	5.923.00	231.819	4	<0.01
		706	obs.	5,529	260	66	34	13	9	12	5,923			
1042	August	44	exp.	2,613.04	41.88	0.98	0.03				2,656.00	0.582	1	>0.05
		44	obs.	2,618	33	4	1				2,656			
1043		108	exp.	2,211.08	90.80	7.13	0.78	0.10	0.01		2,310.00	2.334	2	>0.05
		108	obs.	2,219	80	7	3		1		2,310			
1070		15	exp.	465.42	14.16	0.39					480.00	0.012	1	>0.05
		15	obs.	465	15						480			
1075		55	exp.	1,044.57	48.13	2.92	0.26	0.03			1,096.00	0.602	1	>0.05
		55	obs.	1,050	39	5	2				1,096			
1079		15	exp.	221.74	11.75	1.30	0.18	0.02			235.00	0.408	1	>0.05
		15	obs.	224	8	2	1				235			
Total		237	exp.	6,555.85	206.72	12.72	1.25	0.15	0.01		6,777.00	14.206	2	<0.01
		237	exp.	6,576	175	18	7		1		6,777			
1043	September	39	exp.	2,290.28	36.42	1.18	0.05				2,328.00	0.014	1	>0.05
		39	obs.	2,291	35	2					2,328			
1070		27	exp.	156.88	19.77	2.88	0.41	0.05			180.00	0.483	1	>0.05
		27	obs.	160	14	5	1				180			
1079		118	exp.	2,599.87	102.82	6.64	0.53	0.05			2,710.00	39.481	2	<0.01
		118	obs.	2,617	71	20	1	1			2,710			
Total		184	exp.	5,047.03	159.01	10.70	0.99	0.10			5,218.00	36.868	2	<0.01
		184	obs.	5,068	120	27	2	1			5,218			
1043	October	13	exp.	1,481.38	12.26	0.35	0.01				1,494.00	0.031	1	>0.05
		13	obs.	1,482	11	1					1,494			
1070		33	exp.	788.27	30.49	1.17	0.04				820.00	0.017	1	>0.05
		33	obs.	789	29	2					820			
1079		61	exp.	2,671.87	55.44	2.51	0.16	0.01			2,730.00	1.465	1	>0.05
		61	obs.	2,681	39	8	2				2,730			
Total		107	exp.	4,941.52	98.19	4.03	0.21	0.01			5,044.00	1.094	1	>0.05
		107	obs.	4,952	79	11	2				5,044			
1070	November	10	exp.	906.14	9.69	0.14					916.00	0.002	1	>0.05
		10	obs.	906	10						916			
1079		6	exp.	1,304.04	5.90	0.04					1,310.00	0.000	1	>0.05
		6	obs.	1,304	6						1,310			
Total		16	exp.	2,210.18	15.59	0.18					2,226.00	0.002	1	>0.05
		16	obs.	2,210	16						2,226			

χ^2/df values do not appear to decrease consistently with time, as would be expected if the fish tend to mix gradually with time. If, however, only the values corresponding to date of release-month of recapture strata with more than 10 tag returns are considered the χ^2/df values tend to decrease with time. The χ^2 values corresponding to these strata are summed at the bottoms of the first five sections of Table 6, and these sums are divided by the sums of the degrees of freedom to obtain total χ^2/df values. It can be seen that these also tend to decrease with time. In addition, the χ^2 values and degrees of freedom for the strata with more than 10 tag returns for all the experiments are summed in the last section of Table 6; the χ^2/df values again tend to decrease with time. It thus appears that the fish were gradually mixing as time passed.

One thousand Monte Carlo simulations were run for each stratum with more than 10 tags, using computer program MONTCARL, to determine the probability of obtaining an equal or greater value of χ^2/df, if the tagged and untagged fish were randomly mixed with one another. The results are shown in the last column of Table 6. In most cases these indicated that the tagged and untagged fish were not randomly mixed. These data tend to indicate less rapid mixing with time than do the data for the Chi-square contingency tests.

DISCUSSION

There is a fundamental difference between the two methods. The Chi-square contingency tests test whether the tagged fish occurred in many or few of the schools, whereas the binomial tests test whether the ratios of tagged to total fish are consistent among schools. For example, if there was a total of 15 returns of tagged fish obtained from 15 different sets from a total of 20 25-ton sets and 20 1-ton sets, it would make no difference for the Chi-square contingency tests which sets the tagged fish occurred in. For the binomial homogeneity tests, however, the χ^2/df value would be much greater if the tagged fish occurred in 15 of the 20 1-ton sets than if they occurred in 15 of the 20 25-ton sets.

The Chi-square contingency tests are adversely affected by the small numbers of tag returns, which makes them rather low powered. For example, for the releases of 19 June 1962, and 28 June 1963,

TABLE 6.—Results of binomial homogeneity tests with skipjack tuna tag return data.

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1962	2 June	June	228	33	714.44	3.15	<0.01
		July	174	15	236.33	1.37	>0.05
		August	333	10	1,467.22	4.42	
	3 June	June	223	26	880.38	3.97	<0.01
		July	174	18	272.03	1.57	<0.05
		August	333	10	304.10	0.92	
	4 June	June	212	32	4,395.24	20.83	<0.01
		July	174	15	327.12	1.89	<0.05
		August	333	9	666.62	2.01	
	17 June	June	162	129	7,862.99	48.84	<0.01
		July	174	6	333.26	1.93	
		August	333	1	81.91	0.25	
	18 June	June	152	15	435.92	2.89	<0.01
		July	174	2	466.73	2.70	
		August	333	0	—	—	
	19 June	June	141	95	543.94	3.89	<0.01
		July	174	28	575.73	3.33	<0.01
		August	333	5	236.97	0.71	
	23 June	June	77	95	392.78	5.17	<0.01
		July	174	40	744.76	4.30	<0.01
		August	333	7	533.24	1.61	
	24 June	June	60	14	99.18	1.68	<0.05
		July	174	28	1,592.40	9.20	<0.01
		August	333	2	299.98	0.90	
	Total	June	1,255	439	15,324.87	12.29	
		July	1,044	144	3,748.37	3.61	

TABLE 6.—*Continued.*

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1963	5 June	June	89	26	141.07	1.60	>0.05
		July	282	25	702.74	2.50	<0.01
		August	385	16	1,250.94	3.26	<0.01
		September	388	6	645.62	1.67	
		October	249	1	2,110.73	8.51	
	9 June	June	89	28	293.56	3.34	<0.01
		July	282	50	1,036.42	3.69	<0.01
		August	385	24	514.06	1.34	>0.05
		September	388	6	779.54	2.01	
		October	249	2	314.69	1.28	
	20 June	June	53	12	56.66	1.09	>0.05
		July	282	15	532.52	1.90	<0.05
		August	385	10	681.99	1.78	
		September	388	6	1,105.22	2.86	
		October	249	2	192.00	0.78	
	27 June	June	24	33	197.47	8.59	<0.01
		July	282	101	1,683.31	5.99	<0.01
		August	385	48	1,019.23	2.65	<0.01
		September	388	19	843,91	2.18	<0.01
		October	249	8	258.17	1.05	
	28 June	June	11	31	401.40	40.14	<0.01
		July	282	43	1,071.63	3.81	<0.01
		August	385	5	85.27	0.22	
		September	388	1	268.06	0.69	
		October	249	0	—	—	
	1 July	July	265	14	1,272.38	4.82	<0.01
		August	385	5	1,000.85	2.61	
		September	388	1	447.33	1.16	
		October	249	0	—	—	
	Total	June	266	130	1,090.16	4.16	
		July	1,675	248	6,299.00	3.77	
		August	1,155	88	2,784.23	2.42	
		September	388	19	843.91	2.18	
1973	12 June	June	129	4	125.55	0.98	
		July	144	9	190.46	1.33	
		August	120	4	90.50	0.76	
		September	45	5	77.04	1.75	
		October	205	7	289.43	1.42	
		November	229	1	78.43	0.34	
	13 June	June	118	3	156.86	1.34	
		July	144	8	118.45	0.83	
		August	120	4	256.57	2.16	
		September	45	4	24.50	0.56	
		October	205	13	214.15	1.05	>0.05
		November	229	3	116.14	0.51	
	14 June	June	105	0	—	—	
		July	144	6	333.14	2.33	
		August	120	2	78.99	0.66	
		September	45	8	41.23	0.94	
		October	205	10	387.81	1.90	
		November	229	5	477.96	2.10	
	30 June	July	144	9	344.95	2.41	
		August	120	5	50.35	0.42	
		September	45	10	21.62	0.49	
		October	205	3	324.07	1.59	
		November	229	1	197.57	0.87	
	Total	October	205	13	214.15	1.05	

TABLE 6.—*Continued.*

Year	Date of release	Month of recapture	Sets	Tags	χ^2	χ^2/df	Probability
1975	26 June	July	215	5	192.62	0.90	
		August	274	15	536.17	1.96	<0.01
	20 July	July	51	1	13.23	0.26	
		August	274	8	246.67	0.90	
	21 July	July	42	7	64.87	1.58	
		August	274	10	1,255.33	4.60	
	21 July	July	42	0	—	—	
		August	274	22	1,036.53	3.80	<0.01
	Total	August	548	37	1,572.70	2.88	
1976	9 June	June	297	13	468.83	1.58	>0.05
		July	386	13	874.92	2.27	<0.01
		August	47	1	38.13	0.83	
		September	542	5	628.52	1.16	
		October	546	3	1,830.07	3.36	
		November	262	0	—	—	
	10 June	June	294	26	664.08	2.27	<0.01
		July	386	17	744.88	1.93	<0.01
		August	47	0	—	—	
		September	542	8	578.70	1.07	
		October	546	5	354.91	0.65	
		November	262	1	410.61	1.57	
	17 June	June	252	80	977.05	3.89	<0.01
		July	386	120	1,283.42	3.33	<0.01
		August	47	9	359.63	7.82	
		September	542	48	1,448.02	2.68	<0.01
		October	546	31	1,002.48	1.84	<0.01
		November	262	1	153.34	0.59	
	18 June	June	240	33	1,749.76	7.32	<0.01
		July	386	88	947.11	2.46	<0.01
		August	47	4	399.34	8.68	
		September	542	43	2,018.78	3.73	<0.01
		October	546	18	704.02	1.29	>0.05
		November	262	2	105.17	0.40	
	19 June	June	232	6	249.12	1.08	
		July	386	23	611.28	1.59	<0.05
		August	47	1	292.31	6.35	
		September	542	14	594.33	1.10	>0.05
		October	546	4	771.34	1.42	
		November	262	2	242.38	0.93	
	Total	June	1,083	152	3,859.72	3.58	
		July	1,930	261	4,461.61	2.32	
		September	1,626	105	4,061.13	2.50	
		October	1,092	49	1,706.50	1.57	
all		June	2,604	721	20,274.75	7.84	
		July	4,649	653	14,508.98	3.13	
		August	1,703	125	4,356.93	2.56	
		September	2,014	124	4,905.04	2.44	
		October	1,297	62	1,920.65	1.48	

there were sets with more than five tagged fish in them, and yet the results of the Chi-square tests were not significant. This is caused by the requirement that each category have an expected value of 5 or greater. Accordingly, it is likely that if there had been more tag returns, there would have been more categories for many of the tests and significant results for more of them. The practice of combining the results for fish of the same experiment released on different days ("Total" lines in Table 4) and for fish of different experiments ("Total" lines of Table 5) helps to overcome this weakness. It can be seen in the text table above that the ratios increased with the degrees of freedom. If there were more tag returns, there would be fewer tests with one degree of freedom and more with three or more degrees of freedom, and the ratios of significant tests would almost certainly increase.

On the other hand, the way that the tag return data are handled causes it to appear that there were more sets with more than one tagged fish than was actually the case. Ideally, all tagged fish would be recovered by fishermen as soon as they are caught, and then set aside for later examination by an IATTC employee, and the tag numbers, locations, and dates of recapture would be recorded so that each fish could be assigned to the proper set. In reality, however, less than half the tagged fish recaptured are recovered by the fishermen, and since the fish from different sets are mixed in the wells of the vessels, the chance of assigning tagged fish to specific sets is lost, except when enough fish are caught in one set to fill an entire well. Virtually all of the tagged fish which are not recovered by fishermen are recovered later by unloaders and cannery workers. The unloaders and cannery workers usually inform the IATTC employee to whom they return the tagged fish (or the tag without the fish attached to it) that the fish was found in or had come from a particular well or pair of wells of a particular boat. The IATTC employee who receives the tagged fish or tag records this information, and later another IATTC employee compares this information with an abstract of the vessel's logbook and assigns the fish to the set which contributed the greatest weight of fish of the species in question to that well or pair of wells. For example, if a particular well contained fish from sets with 12, 15, 20, and 13 tons made on 1, 2, 3, and 4 June, respectively, and each included one tagged fish, all recovered by unloaders and cannery workers, all four would be assigned to the 3 June set. This would make it appear that the tagged fish tend to remain together more than is actually the case. Another way to handle a situation such as this would be to allocate the four fish among the four sets in proportion to the weights of fish in them, in this case one to each set. This is not done, however, because tagged fish from the same trip of the same vessel are often returned to the IATTC over a considerable period of time, and it is not feasible to keep the tags for long periods waiting for all of them to be returned before processing them. Furthermore, allocation of tagged fish in the way just described would tend to make it appear that the tagged fish remain together less than they actually do if they are not randomly mixed with the untagged ones.

In addition to the problems created by failure to recover all the tagged fish as soon as they are caught, there are probably problems created by false data. Sometimes the persons recovering tagged fish keep the tags they have recovered over a period of several days, weeks, or even longer, and then return them to an IATTC employee, telling him that they were all recovered that day in the well or pair of wells that was unloaded that day. The likelihood that the data are false can often, but not always, be detected by an alert IATTC employee. When the likelihood that the data are false is not detected, it will appear that the tagged fish remain together more than is actually the case. It is believed that, in spite of attempts to detect data which are likely to be false, some false data are included in the analyses and make it appear that the tagged fish remain together more than is actually the case.

The fact that the numbers of tag returns were small, coupled with the requirement for the Chi-square contingency tests that the categories for the expected numbers of tagged fish be equal to or greater than 5, tends to make it appear that the tagged fish mix more rapidly with the untagged ones than is actually the case. The biases resulting from the mixing of the fish caught in different sets in the same wells and from false data tend to make it appear that the tagged and untagged fish mix less rapidly than is actually the case. Thus the two factors tend to cancel each other out, at least partially, although the first bias may be stronger than the second. If so, the tentative conclusion made above that the tagged and untagged fish mix thoroughly within about 3 to 5 months may be incorrect; that time could be somewhat longer. For the binomial homogeneity tests only the second bias exists, so the rate of mixing of the tagged and untagged fish indicated by these tests is probably somewhat slower than is actually the case.

Sharp (1978) stated that it is likely that skipjack tuna in the same school are "related," but it seems unlikely that tunas could school together for their entire lives, an implication attributed to Sharp (1978) by Lester et al. (1985). During the egg and larval stages, the fish are at the mercy of their environment, and individuals which were together at one time would often be separated by the currents. Furthermore, large tunas of the genus *Thunnus* occur mostly in subsurface waters at depths to nearly 300 m (Suzuki et al. 1977). Although there are areas of greater and lesser concentrations of large, subsurface-dwelling fish, there is no evidence that they form concentrated schools such as those which occur at the surface. The present study indicates that skipjack tuna in the size range of about 3.4 to 7.0 pounds (about 43 to 53 cm in length) of the same school mix randomly with those of other schools

within about 3 to 5 months, or possibly somewhat longer. This is in agreement with the findings of Anonymous (1960) and Lester et al. (1985), but not those of Sharp (1978), discussed at the beginning of this report.

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COMPARISON OF TWO LENGTH-FREQUENCY BASED PACKAGES FOR ESTIMATING GROWTH AND MORTALITY PARAMETERS USING SIMULATED SAMPLES WITH VARYING RECRUITMENT PATTERNS

MARGARIDA CASTRO AND KARIM ERZINI[1]

ABSTRACT

Length-frequency distributions were simulated for species with recruitment patterns characteristic of many tropical fish: 1) one recruitment peak per year, fast growth and very high mortality, 2) one recruitment peak per year, slow growth and moderate to high mortality, 3) two recruitment peaks per year, slow growth and moderate to high mortality, and 4) random recruitment, slow growth and moderate to high mortality. Two microcomputer program packages—one incorporating the ELEFAN I & II programs and the other implementing a form of Modal Progression Analysis—were used to estimate growth and mortality parameters, and these were compared with the initial parameters used to generate the simulated samples. The results, while generally encouraging, suggest that multiple recruitments per year make it difficult to estimate growth and mortality parameters using these two packages.

Information concerning growth, mortality, and recruitment patterns is of great importance in length-frequency analysis. The purpose of this paper was to evaluate two sets of methods used in length-frequency analysis in terms of their ability to produce accurate estimates of growth and mortality parameters in the absence of such biological information.

The methodology chosen consisted of generation of length-frequency distributions with known parameters to which the length-frequency methods were applied. The results obtained with the method were compared with the initial conditions. This procedure has been used in other studies (Hampton and Majkowski 1987; Jones 1987).

The development of the program for simulating length frequencies was guided by assumptions implicit in the length-frequency methods and by known factors concerning the biology of fish. These include 1) average individual growth in accordance with the von Bertalanffy growth curve, 2) little variation in natural mortality throughout the exploited phase, 3) exponential decline in the numbers of a cohort, 4) length distributions normal for each age class, and 5) recruit numbers random. Some other features of the program, such as the selectivity of the gear (logistic type) are not standard assumptions of length-frequency methods but are options for parameters necessary to describe the effect of fishing.

The authors believe that the simulated length frequencies accurately reflect the assumptions of the length-frequency methods and therefore the generated samples can be used to test, correct, and possibly improve these methods. The simulated samples might also help to define a range of situations when a specific length-frequency method can or cannot be used.

Traditionally, length-frequency analysis methods have been used as validation methods for age determinations made independently. Recently, these techniques have grown in importance and frequency of use, in particular in tropical fisheries, where age determinations based on direct reading of check marks in hard parts of the fish are difficult, and in crustaceans, which do not have permanent hard structures. As a result, length-frequency analysis has been used in situations where very little is known about the biology of the species.

It is the purpose of this work to contribute to the understanding of the possible errors that are made when length-frequency analysis is used without biological information on mortality levels, growth parameters, and, in particular, recruitment patterns. It might be argued that such methods of length-frequency analysis are particularly useful in the situations described above, precisely because they do not require a priori knowledge of biological information. The question then becomes, is it legitimate to use length-frequency analysis techniques in the absence of minimum biological information? And if the answer to this question is no, then what

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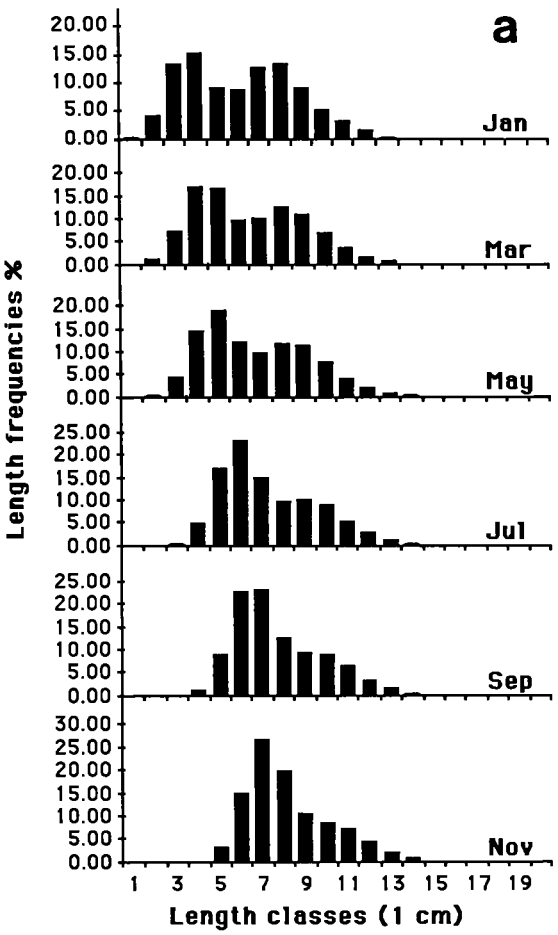
are the minimum requirements for each one of the length-frequency analysis methods? We hope this paper can contribute to providing some understanding of this problem.

MATERIALS AND METHODS

The Simulation Program: SIMULPOP[2]

SIMULPOP was developed in BASIC, for IBM microcomputers and compatibles. Populations are simulated by following cohorts in time and the general characteristics and assumptions of the program include 1) individual growth described by a von Bertalanffy growth curve, no seasonality considered; 2) recruitment: different patterns and random in numbers; 3) natural mortality: random and normally distributed; 4) fishing mortality: random and normally distributed, and corrected for incomplete selectivity in younger ages; 5) selectivity: logistic equation considered to represent selectivity of the fishing gear; and 6) length distribution for each age normally distributed, with a mean given by the von Bertalanffy growth curve. The shapes of the frequency distributions are independent of

[2]The program SIMULPOP is available from Margarida Castro upon request.



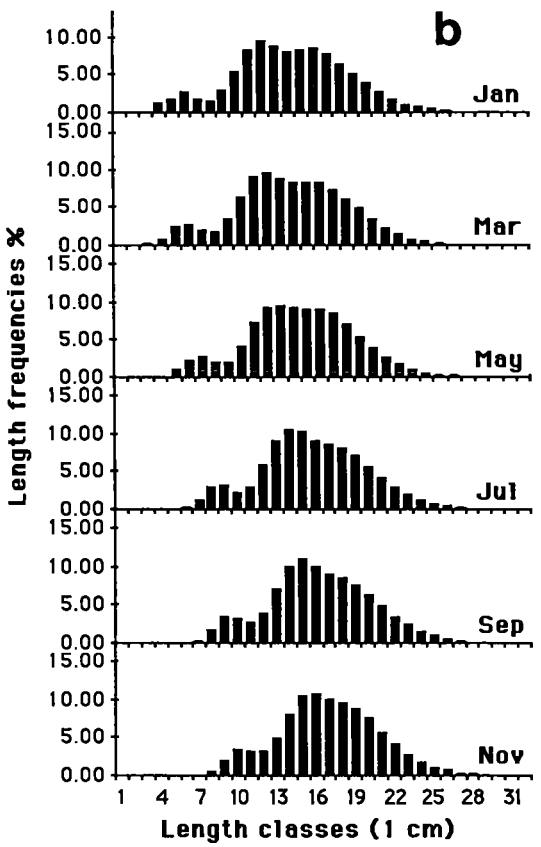


FIGURE 1a.—Example of simulated length-frequency distributions for situation 1, the sardine-type species with one recruitment peak a year. Only 6 of the 12 months are represented.

FIGURE 1b.—Example of simulated length-frequency distributions for situation 2, the sparid/lutjanid-type species with one recruitment peak a year. Only 6 of the 12 months are represented.

catch size and can be regarded as unbiased. Examples of simulated length frequencies for each of the four situations are presented in Figures 1a–d and examples of component distributions contributing to the composition of a particular distribution are given in Figures 2a–d. In what follows, the word cohort refers to the fish recruited in a particular period. For one spawning peak a year cohort and age class are equivalent. However, in the situations where multiple recruitment periods were simulated, more than one cohort will contribute to a given age class. In multiple recruitment situations the word cohort does not have its traditional meaning.

The Choice of Parameters

The following four situations were simulated and the parameters are given in Table 1: 1) A sardine-like species, characterized by small size, fast growth, high mortality, very intense fishing mortality, and with one recruitment peak per year (situation 1); 2) a small sparid/lutjanid type species, with larger size, slower growth with moderate to high fishing mortality, and one recruitment peak per year (situation 2); 3) a species with the same characteristics as the one described previously, but with two recruitment peaks per year (situation 3); and 4) a species with the same characteristics as the two

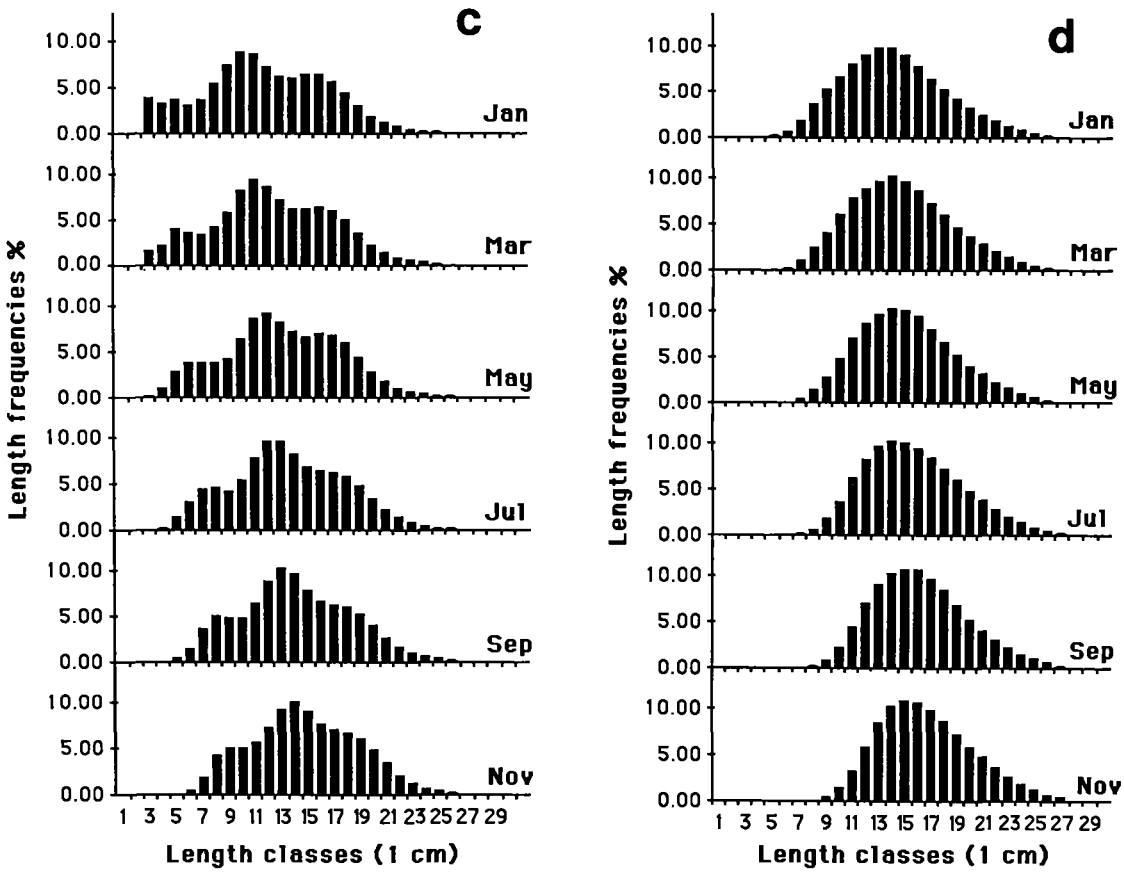
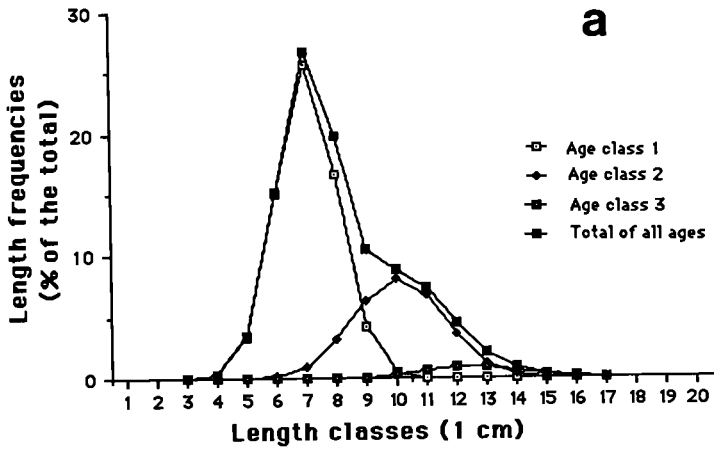


FIGURE 1c.—Example of simulated length-frequency distributions for situation 3, the sparid/lutjanid-type species with two recruitment peaks a year. Only 6 of the 12 months are represented.

FIGURE 1d.—Example of simulated length-frequency distributions for situation 4, the sparid/lutjanid-type species with random recruitment. Only 6 of the 12 months are represented.



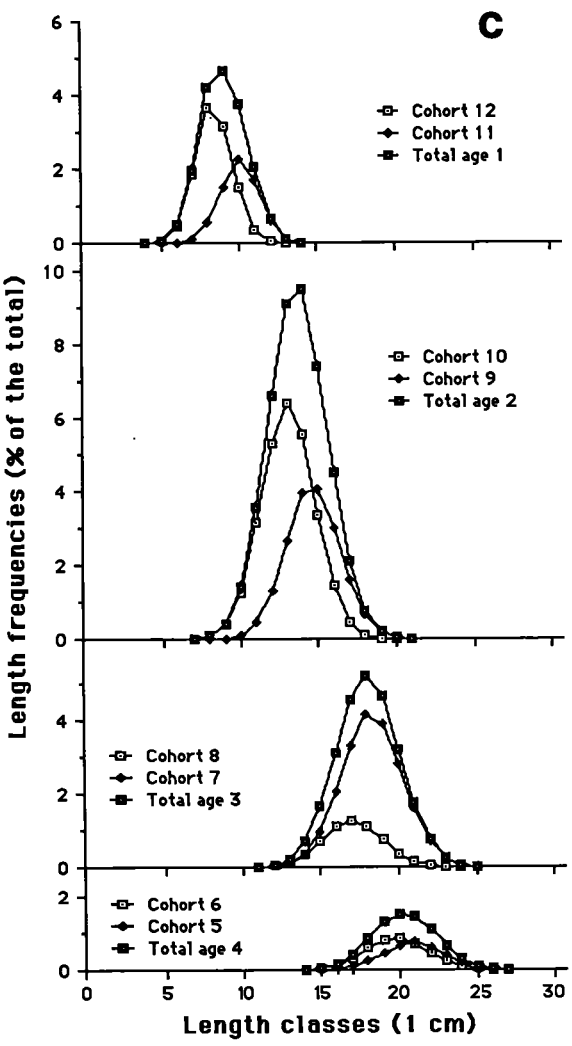
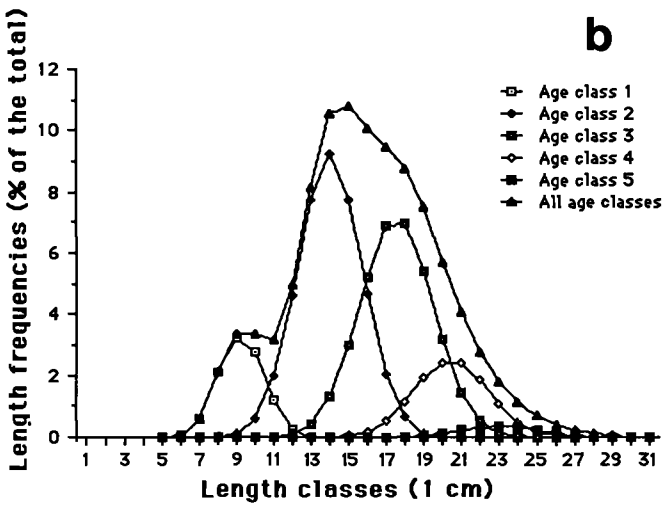


FIGURE 2a.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1a) for situation 1. Age class 4 is not represented due to low frequencies.

FIGURE 2b.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1b) for situation 2. Age class 6 is not represented due to low frequencies.

FIGURE 2c.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1c) for situation 3. There are two cohorts contributing to each age class. Ages 5 and 6 are not represented due to low frequencies.

FIGURE 2d.—Example showing component distributions for one length-frequency sample (month of November of the same simulation represented in Figure 1d) for situation 4. In this case there are multiple cohorts contributing to each age class. Age classes 1 and 6 are not represented due to low frequencies.


b
Length frequencies (% of the total)
Length classes (1 cm)
Age class 1
Age class 2
Age class 3
Age class 4
Age class 5
All age classes

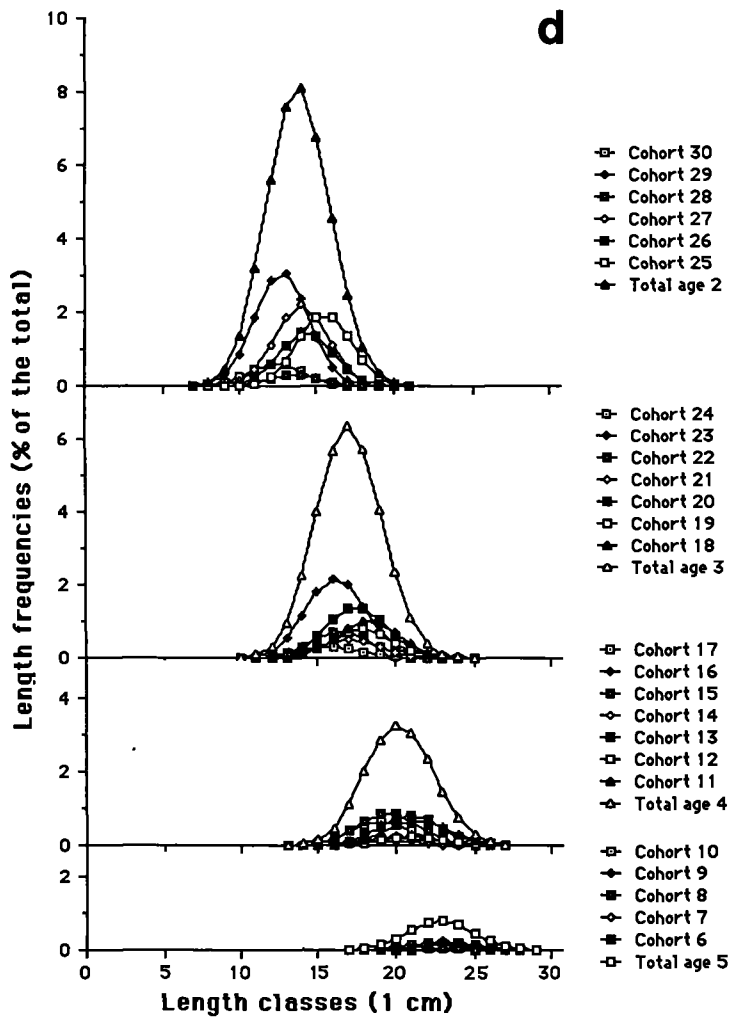

d
Length frequencies (% of the total)
Length classes (1 cm)
Cohort 30
Cohort 29
Cohort 28
Cohort 27
Cohort 26
Cohort 25
Total age 2
Cohort 24
Cohort 23
Cohort 22
Cohort 21
Cohort 20
Cohort 19
Cohort 18
Total age 3
Cohort 17
Cohort 16
Cohort 15
Cohort 14
Cohort 13
Cohort 12
Cohort 11
Total age 4
Cohort 10
Cohort 9
Cohort 8
Cohort 7
Cohort 6
Total age 5

TABLE 1.—Parameters chosen for the simulations.

Situation:	1	2	3	4
Oldest age present in catch (years)	4	6	6	6
Age of recruitment to the area of adult stock (months)	6	6	6	6
Growth parameters				
L_∞ (cm)	20	35	35	35
K	0.3	0.2	0.2	0.2
t_0 (years)	0	0	0	0
Instantaneous annual natural mortality rate				
Mean	0.4	0.25	0.25	0.25
SD	0.015	0.01	0.01	0.01
Instantaneous annual fishing mortality rate				
Mean	1.7	0.8	0.8	0.8
SD	0.05	0.02	0.02	0.02
Selectivity parameters (cm)				
Mesh	1.5	3.5	3.5	3.5
Length 25% retension	3.25	11.25	11.25	11.25
Length 75% retension	8.75	16.75	16.75	16.75
Standard deviations of length-at-age				
Age 0	0.5	1.0	1.0	1.0
Age 1	1.0	1.2	1.2	1.2
Age 2	1.5	1.5	1.5	1.5
Age 3	1.5	2.0	2.0	2.0
Age 4	1.5	2.0	2.0	2.0
Age 5		2.0	2.0	2.0
Age 6		2.0	2.0	2.0
Recruitment pattern	once/yr May-June	once/yr May-June	twice/yr Mar.-Apr. Sept.-Oct.	stochastic

previous ones, but with stochastic recruitment, and random recruitment intensities assigned to randomly selected months (situation 4).

The choice of these recruitment patterns was based on the knowledge that tropical species have different types of recruitment periodicities with varying temporal and spatial variation (Thresher 1984). The same species may have different patterns (Sale et al. 1984). Two principal peaks and year-round recruitment have been reported in coral reef fish from Hawaii (Walsh 1987) and Curaçao (Luckhurst and Luckhurst 1977). One single recruitment per year has also been reported (Li 1960; Gladstone and Westoby 1988).

Mortality values, both natural and fishing, were chosen to have small standard deviations (Table 1) because the main objective was to examine the effects of different recruitment patterns, and we wanted to keep the possible effects of variations in other factors as small as possible.

The standard deviations of length-at-age used (Table 1) are representative of values for species with life history characteristics similar to those of the cases considered for this study (K. Erzini, work in progress).

The Length-Frequency Analysis

The two techniques chosen to represent length-frequency analysis were ELEFAN (Electronic Length Frequency Analysis) (Brey and Pauly 1986) and the package entitled "Length Frequency Based Fish Stock Assessment Microcomputer Programs" (LFSA package) by Sparre (1986; adapted to MS DOS by K. Erzini). ELEFAN has been widely used in the analysis of tropical fish stocks, and its non-parametric basis for determination of K and L_∞ makes it a unique methodology for the analysis of length frequencies.

In ELEFAN, the length-frequency samples are restructured in order to emphasize peaks. Details of the restructuring methodology are given in Brey and Pauly (1986). Growth curves are generated for values of K and L_∞ within specified ranges and fit to the reconstructed length-frequency data. The best curves are considered to be the ones that pass through the most peaks and the least troughs.

The LFSA package uses a method of a different nature—the Bhattacharya method (Bhattacharya 1967), to separate normal curves, under the assumption that the length distributions for each age are

normal. The decomposition of each length-frequency sample into component distributions is carried out by plotting a logarithmic transformation of the differences between successive length frequencies. A normal distribution appears as a series of values making up a straight line with a negative slope. In the LFSA package, which implements the Bhattacharya (1967) method, the user selects the points believed to make up a normal distribution, and the mean, standard deviation and various other statistics are computed. In the next step, the means of all distributions are plotted against time and the mean lengths thought by the user to reflect the progression of a cohort are linked. Finally, growth parameters are computed from the linked modes by a method referred to as a Gulland and Holt plot (Gulland and Holt 1959).

In both packages, the growth parameters are used to create age based catch curves for estimation of instantaneous annual total mortality, Z. Therefore, except for the estimation of Z, the methodologies of the two packages are quite independent. However they are both characterized by a certain degree of subjectivity.

Methodology

Following the suggestion of Hampton and Majkowski (1987), two different teams were formed. One (team A) created the simulated samples (10 cases of 12 monthly samples for each situation), and another (team B) ran the length-frequency analysis. The 40 cases were given arbitrary filenames and were mixed by team A prior to analysis by team B. This was done to avoid influencing the choice of initial values or parameter ranges, required by some of the methods applied. In estimating the growth parameters using the LFSA package, constraints on the limit of acceptable estimates of L_∞ were guided by the value of the midpoint of the largest size class in each particular case. For analysis by ELEFAN I & II, the size of the largest length class also helped guide the choice of range of potential values of L_∞. Team A provided information to team B in different phases. In phase 1, samples were provided to team B with information on mesh size, and only broad descriptions of the type of species, and indications of fishing mortality levels. Team B analyzed the length-frequency samples with both packages to the best of his ability. In Phase 2, exact information on growth, mortality, and number of age classes was provided and new estimates of Z were obtained using both packages. The results produced by team B are presented in Table 2.

It should be noted that expected values for Z in Table 2 are less than the sums of F and M in Table 1. This is because Table 1 values are inputs, and F is subsequently corrected for selectivity.

RESULTS

In situation 1, the sardine-type species with one recruitment peak per annum, the samples were simulated using growth parameters typical of a small clupeid with high fishing effort expressed by a high value of F and small mesh size. Thus a typical length-frequency sample consists of 4 component distributions or 4 cohorts (Figure 2a). While estimates of the growth parameters by ELEFAN were very good, the LFSA package estimates of K were surprisingly high.

Close examination of the length frequencies, the Bhattacharya method and Gulland and Holt plot implemented by Sparre revealed a number of factors

TABLE 2.—Results of estimation of growth and mortality parameters (mean and standard deviation) using ELEFAN and LFBFSA packages. Z_1 and Z_2 are total mortalities calculated using estimated and actual K and L_∞ values.

		ELEFAN				LFBFSA				Expected values		
Situation	Parameters	K	L_∞	Z_1	Z_2	K	L_∞	Z_1	Z_2	K	L_∞	Z
1	Mean	0.30	21.3	2.09	1.78	0.46	21.0	3.01	1.96	0.3	20.0	1.32
	SD	0.03	1.30	0.41	0.26	0.14	3.55	0.67	0.25			
2	Mean	0.18	38.8	1.35	1.22	0.18	33.2	0.89	1.17	0.2	35.0	1.02
	SD	0.02	3.10	0.27	0.14	0.06	2.97	0.33	0.22			
3	Mean	0.19	37.9	1.24	1.17	0.14	36.1	0.79	1.09	0.2	35.0	1.02
	SD	0.03	2.33	0.27	0.18	0.05	3.84	0.38	0.13			
4	Mean	0.19	37.2	1.24	1.15	0.20	36.2	1.15	1.14	0.2	35.0	1.02
	SD	0.04	2.93	0.40	0.20	0.06	4.35	0.20	0.11			

contributing to the high estimates of K. First, the relatively fast growth rate and high mortality resulted in early overlapping or accumulation of distributions and in large fish being rare so that team B could never identify more than 3 out of 4 modes corresponding to fished age classes using the Bhattacharya method in any sample (Fig. 2a). Second, the third mode was consistently overestimated because the distributions for age classes 3 and 4 were merged together. Third, the young-of-the-year fish do not appear in the samples as a well-defined distribution until late in the monthly time series of samples because recruitment does not take place until June. Finally, we found that estimates of K using the Gulland and Holt plot in the LFSA package were very sensitive to small deviations in the estimates of modal lengths obtained using the Bhattacharya method.

Total mortality estimates for situation 1 using the estimated K and L_∞ values were not good for either package. Estimates of Z using the actual K and L_∞ values used in the simulations were within 35% and 45% of the expected Z (Table 2).

Situation 2 was the sparid/lutjanid type, characterized by a single recruitment peak per year and 5 distributions corresponding to the 5 fished cohorts in the catch (Fig. 2b). Both methodologies gave similar estimates of K, close to the actual value. However, L_∞ was overestimated by ELEFAN and underestimated by the LFSA package. The mean estimate of Z was within 32% of the expected Z for the ELEFAN catch curve analysis and within 13% for the LFSA package analysis. Mean Phase II estimates of Z were 20% and 15% above the expected Z (Table 2).

Situation 3, the sparid/lutjanid type with two recruitment peaks per year (Fig. 2c) produced good results using ELEFAN. However, modal progression estimates of K were low, with corresponding underestimates of Z (Table 2). Component distributions were poorly defined compared to situation 2; age classses 4 and 5 were often obscured by the age class 3 distribution. Incorrect separation of distributions and bad estimates of growth parameters were therefore not unexpected.

For the last situation, the sparid/lutjanid type with stochastic recruitment (Fig. 2d), estimates of K, L_∞, and Z were generally good for both packages. However, as shown by the standard deviations, the range of estimates for certain parameters was quite high. This was the case for K estimated by ELEFAN and L_∞ estimated by modal progression analysis in the LFSA package.

DISCUSSION

This preliminary study has shown that, as expected, the structure of the data has a big effect on the estimates derived using length-frequency packages. In general, the results were encouraging. However, it should be noted that the simulated length-frequency distributions can be regarded as representing high-quality samples of the hypothetical populations in terms of lack of bias, sample size, and frequency of sampling. In other words, real life length-frequency data is seldom of this quality.

The modal progression analysis implemented by Sparre (1986) was more sensitive to the structure of the length-frequency samples. Worst results in terms of estimation of growth parameters were obtained under multiple recruitment (situation 3) and fast growth and high mortality (situation 1). A fundamental problem with the Bhattacharya method is the inability to identify modes at the upper end of the size spectrum, particularly when there is fast growth or many age groups. Identification of modes using the Bhattacharya method might have been improved by using smaller size class intervals, particularly for situation 1. However, even when there was little ambiguity in the selection of modes using the Bhattacharya method, it was found that the Gulland and Holt plot for estimating K and L_∞ was very sensitive to small underestimates and overestimates of the modes considered to represent growth over time.

Length converted catch curve estimates of total mortality are highly dependent on the estimated growth parameters. Consequently, estimates of Z generally paralleled estimates of K and L_∞ and were not as good as estimates of Z obtained using the actual simulation values of K. These latter estimates of Z were generally close to actual Z values for all situations despite the fact that the length-frequency data necessarily did not meet steady-state assumptions because of variable recruitment and mortality. However, the variability of mortality rates was deliberately kept small because the primary objective was to examine the effects of different recruitment patterns.

ELEFAN, the Bhattacharya, and the modal progression method of the LFSA package all require subjective decision making by the user. It would seem that ELEFAN is less subjective or that poor choices are less likely to be made by the user than in the selection of modes by the Bhattacharya method and in the choice of modes for the modal

progression analysis implemented in the LFSA package.

We feel that length-frequency analysis should not be used in the complete absence of information on growth and recruitment patterns or with very small data sets. Other important information includes data on migration and seasonal patterns in distribution, and such information should be used to guide sampling programs. Irregular recruitment both in terms of level and pattern may strongly affect the results. Clearly, length-frequency analysis can be a useful tool when used in conjunction with other methods. However, it seems unreasonable to expect such techniques to produce reliable information when the classical methods of fisheries fail or cannot be used. For example, traditionally, growth parameters have been estimated from age-length keys and mortalities derived from the age structure of the catch. In cases where the age-length key cannot be obtained, there is a temptation to obtain growth parameters at any cost using length-frequency analysis. If this is done, great care should be taken to ensure that a minimum amount of biological information exists. The use of length-frequency analysis as a "black box" where a length-frequency distribution goes in from one side and a whole set of biological parameters emerge does not seem correct. If as a first step, the data are plotted and there is no visual evidence of progressing modes, then even if biological information is available, length-frequency techniques should perhaps not be applied at all.

To have a more complete picture of the limitations and usefulness of length-frequency techniques, a much wider range of conditions must be tested. For example, the effect of variations in individual parameters particularly M and F, and in combinations of parameters must be tested. The effects of size class width on length-frequency analysis is also an area which should be investigated. It is the intention of the authors to continue this work in order to examine as wide a range of situations as possible.

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SPECIFYING A FUNCTIONAL FORM FOR THE INFLUENCE OF HATCHERY SMOLT RELEASE ON ADULT SALMON PRODUCTION

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ABSTRACT

The hypothesis of density independent marine survival of salmon has been tested extensively with conflicting results. Unduly restrictive functional form and data deficiency have been suggested as the major contributing factors to the mixed results. Focusing on the issue of functional form selection, this paper utilizes the extended Box-Cox flexible functional form which allows the data to determine the statistical relationship between smolts and adult production without a priori restrictions. The model is applied to Hokkaido chum salmon, *Oncorhynchus keta*, and Oregon coho salmon, *O. kisutch*. Empirical results suggest the existence of density dependence for both Hokkaido chum and Oregon coho salmon. Further, an increasing variability of adult production with respect to an increase in smolts is found for Hokkaido chum salmon but not for Oregon coho salmon.

Two issues pertaining to the relationship between the number of hatchery smolts released and the number of adult salmon returned have been investigated recently in the literature. First, the hypothesis of density independence in the relationship between salmon adults and smolts has been tested. The null hypothesis is a linear relationship between adults returned and smolts released, such that the additional adult salmon produced from an increase in smolts released is constant. The second issue is the relationship between the variability of adult production and the number of smolts released. If, in fact, increases in smolts increase the variability of adults produced, fishery management strategies can be improved by considering the trade-off between the mean and variance of adult salmon returned (Walters 1975; McCarl and Rettig 1983).

The empirical results of the test of density independence have been mixed. Nickelson (1986) provided an excellent discussion of previous results pertaining to the test of density independence for Oregon coho salmon. In short, this hypothesis for marine survival of Oregon coho salmon is rejected by McCarl and Rettig (1983) and Peterman and Routledge (1983), but accepted by Peterman (1981), Clark and McCarl (1983), and Nickelson (1986). In addition, biologists in the Oregon Department of Fish and Wildlife have examined several model specifications and manipulations in data sets and have drawn conflicting conclusions about density independence. This led McCarl and Rettig to suggest that conflicting conclusions are caused by the use of different functional form specifications and to suggest further that resolution of the issue of density independence in Oregon coho salmon requires more refined data. In the case of Hokkaido chum salmon, the null hypothesis of density independence fails to be rejected by McCarl and Rettig.

Regarding the estimation of the variability of adult salmon production, Peterman (1981) pointed out the importance of functional form specification and argued for the use of the multiplicative-error model rather than an additive-error model. McCarl and Rettig (1983) demonstrated that the specification of a multiplicative-error model imposes unwarranted restrictions on the estimation of the variability in adult production. McCarl and Rettig utilized the specification developed by Just and Pope (1978, 1979). As a result, the variability in adult salmon production is estimated and conflicting conclusions of the test of density independence emerged.

It is apparent that functional form specification is critical in the test of density independence and the estimation of variability in adult production. The purpose of this paper is to reexamine these two issues by using the extended Box-Cox flexible functional form. Both Hokkaido chum salmon, *Oncorhynchus keta*, and Oregon coho salmon, *O. kisutch*, data are used in this study.

The next section of the paper discusses the importance of the functional form specification and demonstrates the superior flexibility of the Box-Cox

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functional form compared with the Just-Pope specification used by McCarl and Rettig (1983). The empirical results of the Box-Cox functional form are then discussed and compared with those of McCarl and Rettig.

METHODS

Previous findings of Peterman (1978, 1981) indicate the importance of the assumption made regarding error term in testing the hypothesis of density independence. In the process of examining the effect of the number of released smolts on the production of adults and its variability, Peterman (1981) employed two alternative (additive-error and multiplicative-error) model specifications of the error term:

$$A_1 = C_1 S^{k_1} + V_1 \quad \text{...Additive-error model} \quad (1)$$

$$A_2 = C_2 S^{k_2} \exp(V_2) \quad \text{...Multiplicative-error model} \quad (2)$$

where A_i = adult production of salmon using specification i,
S = number of smolts,
C_i = survival rate parameter in model i,
k_i = density dependence parameter in model i,
V_i = error term for model i.

By applying these two models to several sets of salmon data, Peterman (1981) concluded that the multiplicative-error model appears to generate better statistical results than its counter model. In addition, the results of the multiplicative-error model suggest that an increase in the number of smolts will increase the variation in total adult returns. Because the variability in adult production is not only influenced by the number of smolts but also other factors affecting the survival of smolts such as the body size of released smolts, Peterman (1981) suggested that model (2) should be modified by including more explanatory variables. By following Peterman's suggestion a third model can be specified with the additional variable body size, B:

$$A_3 = C_3 S^{k_3} B^{d_3} \exp(V_3). \quad (3)$$

The mean and variance of adult production for this model can be expressed as

$$E(A_3) = C_3 S^{k_3} B^{d_3} E(\exp(V_3))$$

$$\mathrm{Var}(A_3) = (C_3 S^{k_3} B^{d_3})^2 \mathrm{Var}(\exp(V_3)).$$

The instantaneous rates of change in mean and variance of adult production with respect to smolt body size can be expressed as

$$\partial E(A_3)/\partial B = d_3 E(A_3)/B$$

$$\partial \mathrm{Var}(A_3)/\partial B = 2(\mathrm{Var}(A_3)/E(A_3))\, \partial E(A_3)/\partial B.$$

If body size of smolts is enlarged, one would expect higher yields, $\partial E(A_3)/\partial B > 0$. Since both mean and variance are positive, the above model imposes a restriction that the smolt body size has a positive effect on variability, $\partial \mathrm{Var}(A_3)/\partial B > 0$. This restriction is unwarranted because of lacking theoretical support; rather the effect (positive, negative, or zero) of body size on variability of adult return should be tested empirically. For this reason, McCarl and Rettig (1983) adopt a model developed by Just and Pope (1978, 1979) which can be expressed as

$$A_4 = C_4 S^{k_4} B^{d_4} + C_5 S^{k_5} B^{d_5} \exp(V_4)$$

$$= f(S,B) + h^{1/2}(S,B) \exp(V_4) \quad (4)$$

where $h^{1/2}(S,B)$ is a component of the standard deviation of adult production as shown below.

The mean and variance of adult production for this model can be expressed as

$$E(A_4) = C_4 S^{k_4} B^{d_4} + C_5 S^{k_5} B^{d_5} E(\exp(V_4))$$

$$\mathrm{Var}(A_4) = (C_5 S^{k_5} B^{d_5})^2 \mathrm{Var}[\exp(V_4)].$$

Because the signs of d_4 and d_5 are to be determined in the estimation, the advantage of model (4) over model (3) is that it allows for body size to have a positive effect on mean return and unknown (positive, negative, or zero) effect on the variability of adult production.

There are problems inherent in model (4), however, the first being that this specification produces a constant percentage change (k_4) in adult production when the number of smolts released changes by 1%, a constant output elasticity, ε_{as}. Output elasticity is an economic term which is widely used in measuring the relationship between input (smolt release) and output (adult production) and has the advantage of being unit free. An output elasticity of 1.0 means that an increase in smolt release by 1% will result in the same percentage increase in

adult production, implying density independence. When the hypothesis of density independence is rejected, output elasticity is less than 1.0. Therefore, there is an one-to-one correspondence between the hypothesis of density independence and the value of output elasticity. The purpose of using the concept of output elasticity here is to facilitate the discussion of the restriction inherent in model (4).

There is no theoretical support for imposing the restriction of constant output elasticity, rather it should be treated as a hypothesis to be tested. More important, body size (B) is likely to have a positive effect on the output elasticity, i.e., $\partial \epsilon_{as}/\partial B > 0$. In other words, when body size of smolts is enlarged, the improved ability of enduring unfavorable environmental conditions should increase the incremental return rate of adult salmon. But, a constant output elasticity implies that body size and the output elasticity are independent.

The comparison between model (3) and model (4) centers around the role of body size in the variability of adult production. However, data on body size is unavailable so that the comparison becomes empirically irrelevant. Consequently, the difference between these two models, in essence, rests on model specification. It should also be pointed out that the estimate of $h^{1/2}(S,B)$ is influenced by the functional form of $f(S,B)$ and vice versa, because $h^{1/2}(S,B)$ is the heteroscedastic error term to be handled by the weighted least squares method. It is, therefore, important to select a more general functional form for the mean and variance of adult production in testing the hypothesis of density independence and in estimating the variability in adult production.

The Box-Cox flexible functional form developed by Box and Cox (1964) and extended by Zarembka (1974) has been a popular tool for both discriminating among alternative functional forms and providing added flexible form in model specification (Moschini and Meilke 1984). The extended Box-Cox functional form for relating adult salmon production to smolts and other explanatory variables X (such as upwelling) can be expressed as

$$A^{(\lambda)} = \alpha_0 + \alpha_1 S^{(\mu)} + \alpha_2 X^{(\theta)} + e \qquad (5)$$

$$\text{where } A^{(\lambda)} = \begin{cases} (A^{\lambda} - 1)/\lambda & \text{for } \lambda \neq 0 \\ \ln A & \text{for } \lambda = 0 \end{cases}$$

$$S^{(\mu)} = \begin{cases} (S^{(\mu)} - 1)/\mu & \text{for } \mu \neq 0 \\ \ln S & \text{for } \mu = 0 \end{cases}$$

$$X^{(\theta)} = \begin{cases} (X\theta - 1)/\theta & \text{for } \theta \neq 0 \\ \ln X & \text{for } \theta = 0 \end{cases}$$

$$e \sim \text{NID}(0, \sigma_1^2).$$

Model (5) includes the linear ($\lambda = \mu = \theta = 1$), multiplicative-error or log-log ($\lambda = \mu = \theta = 0$), and log-linear ($\lambda = 0$, $\mu = \theta = 1$) functional forms as special cases. Therefore, models (3) and (4) are special cases of model (5), which allows both nonconstant output elasticity and nonzero effect of X on the output elasticity.[3]

When the variability of adult salmon production is affected by the values of its explanatory variables, the error term has nonconstant variance, i.e., heteroscedasticity. Zarembka (1974) demonstrated that while the Box-Cox model is fairly robust to departures from normality, it is sensitive to heteroscedasticity. Failure to correct for this problem can generate misleading results (Lahiri and Egy 1981). When heteroscedasticity is present, we can also specify a Box-Cox functional form for the variance of the error term in model (5) as the following:

$$e \sim NID(0, h(S,X)\,\sigma_2^2) \qquad (6)$$

where $h(S,X) = \beta_1 S^{(\tau)} + \beta_3 X^{(\xi)}$.

The parameters, α_i, β_i, λ, μ, θ, τ, and ξ can be estimated by maximum-likelihood algorithms (see Appendix for a discussion of the log-likelihood function and estimation methods). The hypothesis of density independence can be tested by estimating the model with the restriction that $\lambda = \mu = 1$ against the unrestricted model.

[3]The superior flexibility of model (5) compared with models (3) and (4) is an important consideration in testing the hypothesis of density independence in light of the following remarks on the comparison of models (1) and (2) in Peterman (1981, p. 1117):

> "This is not to say that model 2 is the 'true' form of natural variability, because there are numerous other models that were not tested here (many of these alternatives cannot be tested in practice)...."

We also cannot claim that the extended Box-Cox functional form can produce the "best" or "true" functional form. There exist other flexible functional forms, such as Fourier (Gallant 1984), and the literature is silent in the comparison of these flexible functional forms.

Even though the Box-Cox functional form was first proposed in 1964, its application and investigation of its statistical properties have not received much attention until recently. Therefore, there are numerous aspects of transformations that merit further study (Box and Cox 1982). Lacking software support also makes its application difficult. Nevertheless, the superior flexibility of the Box-Cox functional form compared with other functional forms used traditionally is evident and its application should be encouraged.

RESULTS

In order to test the hypothesis of density independence for salmon utilizing the extended Box-Cox flexible functional form, the two data sets analyzed by McCarl and Rettig (1983) were also used here. The first data set contains total Hokkaido hatchery chum salmon fry releases and brood year adult returns for the years 1950 through 1969 (Moberly and Lium 1977). The second data set pertains to Oregon coho salmon for the years 1960 through 1980 (Oregon Department of Fish and Wildlife 1982). This latter data set was also analyzed by Clark and McCarl.

Hokkaido Chum Salmon Results

Due to the lack of data on body size and other factors affecting the survival rate of fry, adult production (in thousands) is estimated with the single explanatory variable, number of fry released (in millions). As explained in the Appendix, the dependent variable is divided by its geometric mean of 3,332,440. The iterated weighted least squares method produces the following maximum log-likelihood results with the t-statistics given in parentheses below the coefficients:

$$A^{(-0.4)} = \underset{(-4.07)}{-1{,}254} \; \underset{(4.07)}{-1{,}756.3S^{(-1.4)}} \qquad (7)$$

$R^2 = 0.48$, Durbin-Watson = 1.5, Log-likelihood = −7.89.

The weight used to remove heteroscedasticity is $S^{(1.06)} = (S^{1.06} - 1)/1.06$. This implies that as the number of fry is increased by 1%, the standard deviation of the adult production increases by 1.06%, which is much smaller than the 2.5% reported by McCarl and Rettig (1983).

The above results suggest that the output elasticity[4] of fry is $1{,}756.3A^{0.4}S^{-1.4}$. When evaluated at the mean values of A and S (which are 1.1278 and 288.36, respectively), a percentage increase in the number of fry increases the adult production by 0.66%, implying density dependence. In addition, this output elasticity is a decreasing function of fry releases. In contrast to these results, McCarl and Rettig (1983) reported a constant output elasticity of 1.09 which was not found to be statistically different from 1.0, supporting density independence.

The hypothesis of density independence was formally tested by estimating the linear relationship between A and S (i.e., the power transformations for A and S are restricted to be one) by using the weighted least squares method (S was treated as the weight) with the following results:

$$A = \underset{(0.6)}{0.18} + \underset{(2.84)}{0.0034S} \qquad (8)$$

$R^2 = 0.31$, Durbin-Watson = 1.04, Log-likelihood = −12.56.

The weighted least squares method produces a Durbin-Watson value of 1.04 which is below the lower limit of its critical value, suggesting the possible existence of autocorrelation. However, the Durbin-Watson value is well known to be below the lower limit (or above the upper limit) which could be the cause by model misspecification or autocorrelated error terms. Because the use of improper functional form is a model misspecification, the extended Box-Cox functional form needs to be explored before assuming the existence of an autocorrelation problem in light of low (or high) Durbin-Watson statistics. The extended Box-Cox results have a Durbin-Watson statistic of 1.50 (implying no autocorrelation), and hence, it is concluded that the low Durbin-Watson value in Equation (8) is a result of incorrect functional form. Since the Durbin-Watson statistic is for detecting first-order autocorrelation, the least squares procedure described in Pagan (1974) was applied to test higher-order autocorrelation. It is concluded that the Box-Cox results are free from autocorrelation problems, first or higher orders.

The hypothesis of density independence can be tested by comparing the log-likelihood values of Equations (7) and (8). The test statistic of twice the difference between the log-likelihood functions under the two specifications follows a chi-square distribution with the number of degrees of freedom equal to the number of restrictions (Theil 1971). This test procedure is similar to the Akaike Information Criterion (Akaike 1974) and has the advantage of testing the significance of the difference between the log-likelihood functions of different model specifications. It is concluded that the density-indepen-

[4]Equation (7) can be written as

$(A^{-0.4} - 1)/(-0.4) = -1254 + 1756.3(S^{-1.4} - 1)/(-1.4)$, or $A^{-0.4} = 0.8 + 501.8S^{-1.4}$.

Output elasticity $\varepsilon_{os} = (\%\Delta A)/(\%\Delta S) = dA/dS)\ (S/A) = 1{,}756.3S^{-1.4}A^{0.4}$ $d\varepsilon_{as}/dS = -2{,}458.8S^{-2.4}A^{0.4} < 0$.

dence hypothesis can be rejected at a 1% level with a critical value of 9.21 at 2 degrees of freedom.

For comparison purposes, the Hokkaido chum salmon data was used to fit the multiplicative-error model (model (2)) by applying the weighted least squares method with the following results:

$$\ln(A) = \underset{(2.06)}{-3.27} + \underset{(2.06)}{0.583}\ln(S) \qquad (9)$$

$R^2 = 0.19$, Durbin-Watson = 1.15, Log-likelihood = −11.22.

By comparing the values of the log-likelihood function of Equations (7) and (9), it can be concluded that the multiplicative-error model can be rejected a 5% significance level. Even though the multiplicative-error model produces a bigger log-likelihood value than the linear model, the difference between these two log-likelihood values is not statistically signifi-

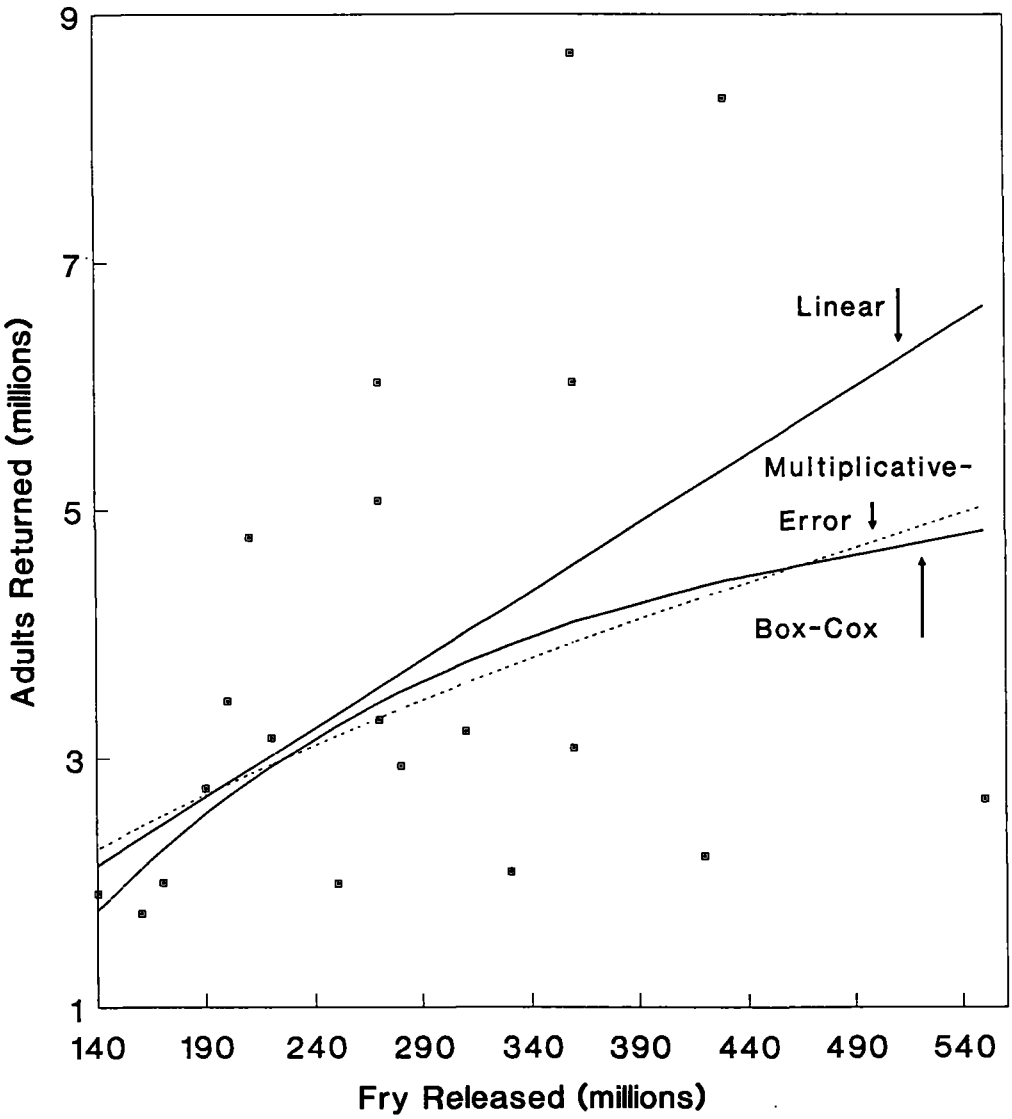

FIGURE 1.—Plot of Hokkaido chum salmon data and estimated relationships: 1950–1969. Dots are actual observations, linear model is Equation (8), multiplicative-error model is Equation (9), and Box-Cox model is Equation (7).

cant. Figure 1 shows the data set with estimated relationships, Equations (7)–(9), superimposed. It is evident that the Box-Cox specification produces a relationship of much bigger curvature and better fit than the multiplicative-error specification.

Oregon Coho Salmon Results

McCarl and Rettig (1983) suggested that aggregated (wild and hatchery) adult coho salmon production (in thousands) is affected by smolt releases (in millions), S, and upwelling index, U. The flexible functional form for Oregon coho salmon can be expressed as Equation (5). The model was estimated by iterated ordinary least squares with the following maximum log-likelihood results:

$$A^{(-0.6)} = \underset{(-1.17)}{-50.08} + \underset{(1.08)}{93.71}S^{(-2.0)} + \underset{(3.37)}{0.59}U^{(0.0)} \quad (10)$$

$R^2 = 0.51$, Durbin-Watson = 2.07, Log-likelihood = −1.66.

To detect any violations of the assumption regarding the homoscedastic error term, a series of tests were conducted by running regressions of squared residuals ($\hat{e}^2$) or logs of ($\hat{e}^2$) on the predicted values of A or the explanatory variables S and U. The regression of $\hat{e}^2$ on all explanatory variables is known as the Breusch-Pagan-Godfrey test and the regression of $\log(\hat{e}^2)$ on all explanatory variables are known as the Harvey test (White 1987). Five tests were conducted using the chi-square distribution, and the assumption of homoscedastic error fails to be rejected at a 5% significance level. The same conclusion is reached when model (2) was fitted by Peterman (1981). The Box-Cox results are also found to be free from autocorrelation problems, first or higher orders.

Empirical results as summarized in Equation (10) indicate that the number of smolt released contributes positively to adult production at a 15% significance level. Upwelling also positively affects adult production at a 1% significance level. The Box-Cox results produce a nonlinear relationship between adult production and smolt release and an output elasticity of less than one, suggesting that the null hypothesis should be rejected. To formally test the hypothesis of density independence, the power transformations for A and S are restricted to be 1.0 and the Box-Cox functional form is re-estimated with the following results:

$$A = \underset{(-1.2)}{-0.58} + \underset{(0.1)}{0.00065}S + \underset{(3.6)}{0.084}U^{(0.39)} \quad (11)$$

$R^2 = 0.41$, Durbin-Watson = 2.09, Log-likelihood = −6.54.

By comparing the values of the log-likelihood functions for Equations (10) and (11) and following a chi-square test with 2 degrees of freedom, it is concluded that the hypothesis of density independence for Oregon coho salmon can be rejected. The same conclusion was reached by Peterman and Routledge (1983) and McCarl and Rettig (1983).

CONCLUSION

The findings of testing the hypothesis of density-independent marine survival for salmon and of the effect of the number of smolts released on the variability of adult production have important implications for fishery managers as noted in the literature. If the hypothesis of density independence fails to be rejected, there is no technical maximum[5] for the adult production from releasing smolts. A technical maximum of adult production exists when the number of smolts has a positive and decreasing effect on adult production. If the variability of adult production is positively affected by the number of smolts, it will be useful for fishery managers and the fishing industry to know the form of variability to evaluate the effectiveness of salmon hatchery operations. Further, fishery managers can improve management strategies by considering the trade-off between the mean and variance of adult production. The hypothesis of density independence has been tested extensively for different sets of data with conflicting results. Functional form selection and data deficiency have been suggested as the causes of conflicting findings.

Results of this study confirm that functional form selection is critical in testing the hypothesis of density independence and estimating the form of the variability of adult production. By using the extended Box-Cox functional form, it is concluded that there exists a density-dependent relationship be-

[5]A "technical maximum" refers to the maximum adult production in physical terms. This may not be an appropriate objective for fishery managers to achieve, because the release of smolts at technical maxima may not generate maximum benefits to the fishing industry. Maximization of the return to hatchery operations appears to be a more suitable objective of a single-attribute model to be accomplished without considering the risk factor.

tween the adult production and the number of chum salmon fry released in Hokkaido. Also, as the number of fry increases, the variability in adult production increases as well. The results reported by McCarl and Rettig (1983), using the Just-Pope specification (a special case of extended Box-Cox), conclude that the hypothesis of density independence fails to be rejected and the effect of the number of fry on the variability of adult production is more than twice that of this study. The Box-Cox results of aggregated Oregon coho salmon also indicate density dependence, and the same conclusion is also reached by McCarl and Rettig (1983) and Peterman and Routledge (1983). Because Nickelson (1986) reached a different conclusion using disaggregated data, the use of the extended Box-Cox specification to analyze disaggregated data for Oregon coho salmon is, therefore, recommended by the authors as a possible research need. However, partitioning the data set according to high and low upwelling, for example, will lead to the problem of insufficient degrees of freedom, as pointed out by an anonymous reviewer. This can be overcome only after a sufficient number of years of data collection have transpired. Finally, data reliability needs to be secured before the selection of functional form can improve our understanding of this issue.

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APPENDIX

Because the estimation of the extended Box-Cox functional form is carried out by maximum likelihood procedures, the log-likelihood function for the extended Box-Cox functional form and estimation methods are briefly presented in this appendix.

Under the assumptions that S and B are nonstochastic and the error term is normally and independently distributed with zero mean and constant variance, σ_1^2, the log-likelihood function of model (5) can be expressed following Spitzer (1982):

$$L(\alpha, \lambda, \mu, \theta, \sigma_1^2) = -T/2(\ln 2\pi + \ln \sigma_1^2) - (2\sigma_1^2)^{-1}(e'e) + (\lambda - 1)\Sigma \ln A \tag{12}$$

where T is the number of observations. To reduce the dimension of the estimation problem, the parameter σ_1^2 can be eliminated from Equation (12) to derive the concentrated log-likelihood function as follows:

$$L(\alpha, \lambda, \mu, \theta) = -T/2(\ln 2\pi + \ln \hat{\sigma}_1^2) + (\lambda - 1)\Sigma \ln A$$

where $\hat{\sigma}_1^2 = (1/T)\hat{e}'\hat{e}$.

When heteroscedasticity is present, the concentrated log-likelihood function for model (5) and the error term expressed in model (6) can be expressed as

$$L(\alpha, \lambda, \mu, \theta) = -T/2(\ln 2\pi + \ln \hat{\sigma}_2^2 + 1)$$

$$- \Sigma \ln (\beta_1 + \beta_2 S^{(\tau)} + \beta_3 B^{(\zeta)}) + (\lambda - 1)\Sigma \ln A \tag{14}$$

where $\hat{\sigma}'^2_2 = (1/T)\hat{e}'V^{-1}\hat{e}$ and V is a nxn matrix (n is the number of observations) in which off-diagonal elements are zeros and diagonal elements are $\beta_1 + \beta_2 S^{(\tau)} + \beta_3 B^{(\zeta)}$.

The maximum log-likelihood parameter estimates for (α, λ, μ, θ, and β) can be obtained by nonlinear least squares methods or iterated ordinary (weighted) least squares procedures. Seaks and Layson (1983) provide an example of the iterated ordinary (weighted) least squares method using the Time Series Processor (TSP) computer package for estimating Box-Cox flexible functional form with standard econometric problems; i.e., heteroscedasticity and autocorrelation.

As Spitzer (1984) pointed out, the ordinary least squares method underestimates the variance of the error term while the first derivative only gradient estimation methods (e.g., Marquardt) overestimate the variance. In order to compress the range of under- and overestimation of the error variance, Spitzer suggested that the dependent variable be divided by its geometric mean. This scaling process will then eliminate the last term in the concentrated log likelihood function in Equations (12)–(14).

AGE, MORPHOLOGY, DEVELOPMENTAL BIOLOGY, AND BIOCHEMICAL GENETIC VARIATION OF YUKON RIVER FALL CHUM SALMON, *ONCORHYNCHUS KETA*, AND COMPARISONS WITH BRITISH COLUMBIA POPULATIONS

TERRY D. BEACHAM, CLYDE B. MURRAY, AND RUTH E. WITHLER[1]

ABSTRACT

Fall chum salmon, *Oncorhynchus keta*, populations spawning in the Yukon River drainage were surveyed for variation in age, size and shape at maturity, developmental biology, and biochemical genetics. Yukon River fall chum salmon matured at older ages and smaller sizes than chum salmon in British Columbia. They also had proportionately smaller heads, thinner caudal peduncles, and smaller fins than British Columbia chum salmon, perhaps illustrating morphometric adaptation to long distance freshwater migration. Yukon River chum salmon were less fecund and had smaller eggs than those in British Columbia, and they also tended to have faster development to alevin hatching and fry emergence than most British Columbia populations. Maximum alevin and fry size of Yukon River salmon occur at lower water temperatures during development than for most British Columbia populations, possibly indicating a developmental adaptation to low winter water temperatures. Genetic differentiation among chum salmon populations in the Yukon River drainage was observed.

The Yukon River is a major North American river, originating in British Columbia and flowing over 3,200 km through the Yukon Territory and Alaska to the Bering Sea, and draining an area of approximately 860,000 km^2. Five species of Pacific salmon (*Oncorhynchus*) occur in the Yukon River (Gilbert 1922), but chinook, *O. tshawytscha*, and chum salmon, *O. keta*, are the most abundant and are exploited in commercial and subsistence fisheries (McBride et al. 1983). Chum salmon in the Yukon River are characterized by distinct seasonal races (Gilbert 1922). The early-maturing or "summer" chum salmon return to the Yukon River between early June and mid-July and spawn in the lower 800 km of the drainage (Buklis 1981). Later-maturing or "fall" chum salmon enter the Yukon River from mid-July through late August and spawn in the up-river portions of the drainage, migrating as far as 2,800 km upstream (Milligan et al. 1986). Fall chum salmon are also larger than summer chum salmon (Buklis 1981; Buklis and Barton 1984), and generally have higher fecundity and younger age compositions than summer chum salmon (Sano 1966).

Chum salmon generally spawn in rivers only a short distance from salt water (≤200 km), a trait very different from the long distance freshwater migrations of Yukon River fall chum salmon. Yukon River fall chum salmon are noted for their high oil content upon entering the river (Gilbert 1922), an adaptation necessary to provide sufficient energy reserves for the freshwater migration, as in Amur River chum salmon in the Soviet Union (Nikol'skii 1961). Adaptations in other biological characters may reflect the environmental conditions experienced by Yukon River fall chum salmon. Thus we examined the variation in life history traits of Yukon River fall chum salmon, and compared this variation to that found in chum salmon in British Columbia.

In 1984, we began a survey of variation in biological characters of fall chum salmon in the Yukon River. Regional biochemical genetic variation had previously been reported for chum salmon in British Columbia (Beacham et al. 1987), and we investigated the biochemical genetic differentiation of Yukon River fall chum salmon. We had previously examined the adaptive nature of the variation in some morphometric and life history traits of chum salmon in British Columbia (Beacham and Murray 1987) and used this for comparison for Yukon River fall chum salmon.

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METHODS AND MATERIALS

Age and Morphology

Chum salmon were collected with gill nets. After capture in 1984, postorbital-hypural length (Vladykov 1962), caudal peduncle depth, and length of the base and height of the anal and dorsal fins were all recorded on the left side in the field to the nearest millimeter. The number of gill rakers on the left anterior arch was recorded, as well as the number of branchiostegal rays on the left side. Five scales and two otoliths were collected from each individual for age determination, and the sex of an individual was confirmed by internal inspection. When the age of an individual estimated from scales and from otoliths disagreed, the age determined from scales was assigned. In 1985, only postorbital-hypural length and sex were recorded for individuals, and only scales were collected for age determination.

Population differences and sexual dimorphism in the meristic characters were examined by two-way analysis of variance, with population and sex as the indices. Population is used in the manner as described by Ricker (1972), as a group of fish spawning in a particular river at a particular season, and there is no substantial interbreeding with another group spawning in a different river. Morphometric measurements of both males and females were standardized to a postorbital-hypural length of 520 mm by the method outlined by Beacham and Murray (1983):

$$M_t = M_o \left(\frac{\bar{L}}{L_o} \right)^b$$

where M_t = size of standardized morphometric character,
M_o = observed character size,
$\bar{L}$ = length that characters are standardized to (520 mm),
l_o = observed postorbital-hypural length, and b is the regression coefficient of $\log_e M_o$ on $\log_e L_o$ (stocks and sexes separate).

Two-way analysis of variance was again used to examine population differences and sexual dimorphism in the morphometric characters.

Developmental Biology

We estimated fecundity of Yukon River chum salmon by collecting and freezing both ovaries from 14 females in the Dawson City commercial fishery in 1985 (we also collected length and scales); we subsequently thawed both ovaries and made total egg counts for each female. The methodology of the survey of developmental biology was similar to that outlined by Beacham and Murray (1987). Gametes were collected from five male and five female Kluane River chum salmon on 17 October 1985. The gametes were then shipped to the laboratory on ice, the eggs fertilized at 8°C, and then subsequently reared in controlled water temperatures of 4°, 8°, and 12°C in vertical stack incubators. Five full-sib families were obtained from the crosses, with each family replicated in each incubator. Water temperatures were recorded daily, and mean temperatures in the incubators during the study were 4.1° (SD = 0.29), 8.0° (SD = 0.44), and 12°C (SD = 0.40), respectively.

Egg diameter (millimeters) and weight (milligrams) for each female were determined from 30 water-hardened eggs preserved for at least 3 months in 10% formalin. During incubation, dead eggs were removed from each family, stored in Stockard's solution, and later inspected to remove unfertilized eggs. Egg survival rates were then calculated based upon the number of eggs initially fertilized. Once hatching began in each family, we recorded the number of newly hatched alevins daily, and within 1 day of 50% hatching we anesthetized and preserved 30 per family in 10% formalin for subsequent determination of alevin length and weight. Fork length was recorded to the nearest 0.1 mm, total weight recorded to the nearest milligram, the yolk separated from the rest of the body and weighed (milligrams), and then tissue weight (milligrams) determined by subtraction. Dead alevins were also removed and counted in order to determine alevin survival rates. The timing of fry emergence (swim-up) for each family was determined by placing the alevins in an emergence trap modified from Mason (1976), where the alevins were classified as newly emergent fry only when they became neutrally buoyant and positively phototactic. When 50% of the fry from a particular family had emerged, all of the family remaining in the incubator was anesthetized and then preserved in 10% formalin, and 30 fry were randomly drawn from the preserved samples and fry length and weight determined as for alevins.

Variation in egg size was analyzed with a one-way (female was the index) analysis of variance. Variation in survival rates was analyzed by first determining survival rates for each group as proportions and then transforming them to radians with the arcsine

square root transformation to normalize the data. We then used an analysis of variance model:

$$Y_{ijkl} = \mu + T_i + F_j + TF_{ij} + R_{ijk} + e_{ijkl}$$

where Y_{ijkl} = transformed survival rate,
μ = overall mean,
T_i = fixed effect of temperature (i = 1–3),
F_j = random effect of family (j = 1–5),
TF_{ij} = random interaction between temperature and family,
R_{ijk} = random effect of replicate (k = 1–2), and
e_{ijkl} = error term for lth observation in subgroup ijk.

Variation in alevin and fry size characters was analyzed with the same model. Satterthwaite's (1946) approximation was necessary to calculate an appropriate mean square to test the effect of family.

Biochemical Genetics

Biochemical genetic sampling began on Canadian populations in 1984 and was expanded in 1985 to include United States populations (Fig. 1). Methodology of sample collection has been outlined by Beacham et al. (1985). Summarized briefly, heart, liver, and muscle samples were collected from adult chum salmon, frozen, and stored at −20°C for later electrophoretic analysis by a consultant. We verified the scoring of all gels from a complete photographic record. Horizontal starch gel electrophoresis, described by Utter et al. (1974), was used to detect protein variation. The loci and buffer systems used

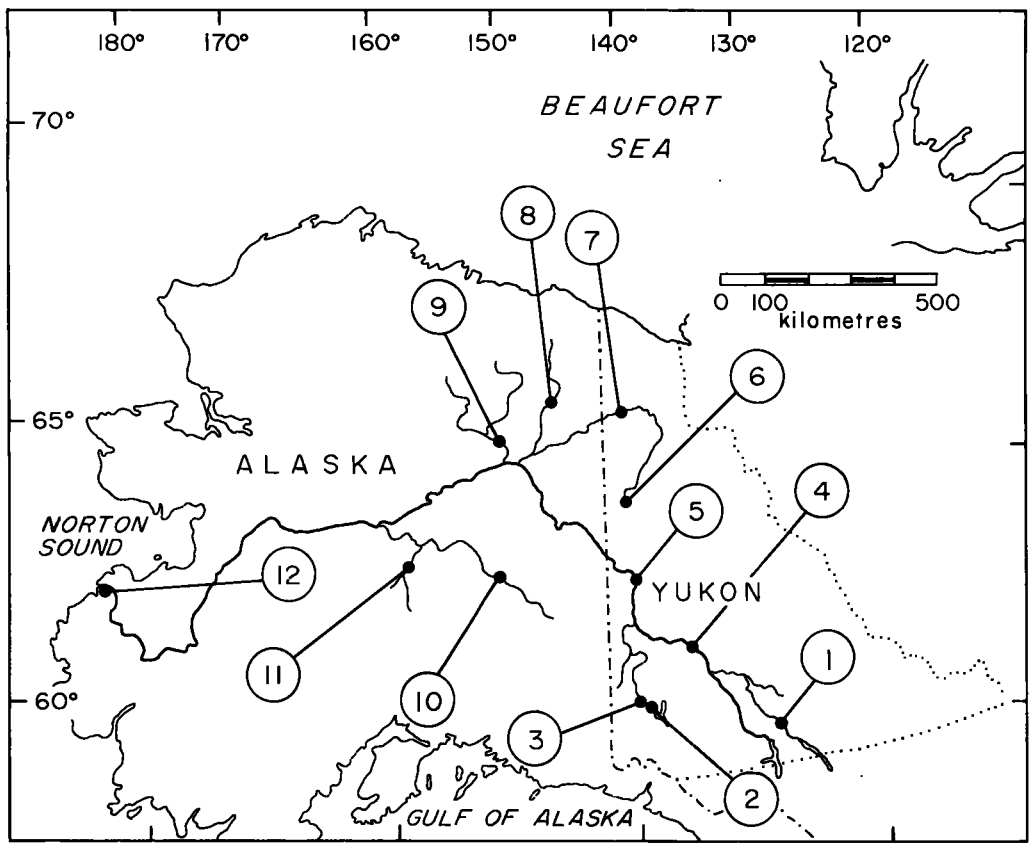

FIGURE 1.—Locations in Yukon River drainage where chum salmon were sampled during 1984–1986. Listed in ascending order are (1) Teslin River, (2) Kluane River, (3) Koidern River, (4) Yukon River at Minto, (5) Dawson City, (6) Fishing Branch River, (7) Porcupine River at Old Crow, (8) Sheenjek River, (9) Chandalar River, (10) Delta River, (11) Toklat River, (12) Yukon River at Emmonak.

are outlined in Beacham et al. (1985). *Lgg* was renamed as Tapep and was scored as a four-allele locus (L. Seeb[2]) (although only three were present in the stocks we surveyed) on both a Tris-boric acid-EDTA buffer described by Markert and Faulhaber (1965) and an amine citrate buffer described by Clayton and Tretiak (1972). *Me* was renamed as *MdhP*, *6-Pg* as *Pgdh*, *Pmi* as *Mpi*, and *Agp* as *G3pdh*.

We determined allelic frequencies for each locus by summing the numbers of each allele and dividing by the total number of alleles counted. Genotypic frequencies at each polymorphic locus in each population were tested for departures from Hardy-Weinberg equilibrium by chi-square. We used the log-likelihood ratio statistic (*G*-test) (Sokal and Rohlf 1969) to test equality of allelic frequencies between countries, among populations within countries, and between years for samples taken from the same population. An approximate *F*-ratio (*G*-statistic summed over all loci/degrees of freedom) was used to test the relative magnitude of the sources of variation. We calculated genetic distance among populations using Nei's (1978) statistic and the 7 loci indicated in Table 7 and constructed a denogram from the matrix of the distances using the unweighted pair group mean method of Sneath and Sokal (1973).

RESULTS

Age and Morphology

Age of Maturity

The dominant age of maturity for fall chum salmon returning to Canadian rivers during 1984 and 1985 was four years, with age 3 and age 5 chum salmon each comprising less than 15% of the total return (Table 1). The proportion of chum salmon returning at three or five years of age varied annually within a population, possibly reflecting different production from the respective brood years. Yukon River chum salmon matured at a significantly older age than chum salmon in British Columbia (X_2^2 = 193.9, $P < 0.01$), but four years was the dominant age of maturity in both areas. Of 227 chum salmon sampled in 1984 from which age could be determined from both otoliths and scales, the same age was recorded in 184 (83%) of the cases. For the 43 other fish, the age estimated from scales was one year older than that estimated from otoliths in 22 cases, whereas in the remaining 21 fish, the age estimated from otoliths was either one year (19 cases) or two years (2 cases) older than that estimated from scales. In 1984, age could not be determined from 16% (48 fish) of the scales collected and 9% (26 fish) of the otoliths collected. In 1985, age could not be determined from 18% (124 fish) of the scales examined due to scale resorption. Age of maturity was more likely to be determined from otoliths than from scales.

TABLE 1.—Percentage of chum salmon returning at ages 3–5 years and mean age of return for Yukon River populations sampled on the spawning grounds during 1984–85. The mean for British Columbia chum salmon was derived from Beacham and Murray (1987).

Population	Year	N	Age (yr) 3	4	5	Mean age (yr)
Yukon River						
Kluane	1984	100	16.0	78.0	6.0	3.90
	1985	96	29.2	70.8	0.0	3.71
Total		196	22.4	74.5	3.1	3.81
Minto	1984	100	13.0	69.0	18.0	4.05
	1985	99	25.3	72.7	2.0	3.77
Total		199	19.1	70.9	10.0	3.91
Fishing Branch	1984	100	14.0	82.0	4.0	3.90
	1985	77	1.3	72.7	26.0	4.25
Total		177	8.5	78.0	13.5	4.05
Porcupine	1985	67	1.5	85.1	13.4	4.12
Teslin	1985	64	0.0	56.3	43.7	4.44
Koidern	1985	81	0.0	74.1	25.9	4.26
Total						
Mean		784	12.5	73.7	13.8	4.01
British Columbia						
Total						
Mean		11,749	32.4	62.1	5.5	3.73

Meristics

No sexual dimorphism was observed in the number of gill rakers or branchiostegal rays ($P > 0.05$). No population differences in gill raker number were observed ($P > 0.05$), but significant differences among populations were observed in branchiostegal ray number ($F_{2,297}$ = 4.36, $P < 0.05$). The population with the greatest number of gill rakers (Fishing Branch) also had the greatest number of branchiostegal rays (Table 2). Yukon River chum salmon had more gill rakers and branchiostegal rays than the average British Columbia chum salmon.

Morphometry

Yukon River male chum salmon were longer than

[2]University of Idaho, Moscow, ID 83843, pers. commun. December 1985.

females at all ages examined ($P < 0.05$) (Table 3). Although there could be significant variation in mean length-at-age among populations ($P < 0.05$), Yukon River chum salmon were substantially smaller than chum salmon of the same age spawning in British Columbia ($P < 0.05$). Size differences between Yukon River and British Columbia chum salmon increase with age, with age 3 Yukon River males 94% of the length of age 3 British Columbia males, but age 5 Yukon River males are 86% of the length of their British Columbia counterparts. Similar results were also observed for females.

We examined whether there was any differentiation of selected morphometric characters with respect to sexual dimorphism or distance of freshwater migration. With the morphometric measurements of both males and females standardized to a postorbital-hypural length of 520 mm, males had longer postorbital head lengths, thicker caudal peduncles, longer base length of the dorsal fin, and longer dorsal and anal fins (all $P < 0.05$) (Table 4). No sexual dimorphism in base length of the anal fin was observed. Significant population differences in the relative sizes of the morphometric characters were also observed, with the Kluane River population having the relatively smallest characters, and the Fishing Branch River population having the proportionately largest characters.

Substantial differences exist in length of freshwater migration between Yukon River fall chum salmon and chum salmon in British Columbia. The relative sizes of the morphometric characters examined are all smaller for Yukon River chum salmon than for chum salmon in British Columbia (Table 4), perhaps illustrating morphometric adaptation of Yukon River chum salmon to the long freshwater migration.

TABLE 2.—Mean number of gill rakers on left anterior gill arch and mean number of branchiostegal rays on left side for Yukon River fall chum salmon sampled during 1984. Standard error of mean is in parentheses. One hundred fish were sampled per population. Data for 9,206 British Columbia chum salmon are from Beacham and Murray (1987).

Population	Gill rakers	Branchiostegal rays
Yukon River		
Kluane	22.88 (0.10)	13.72 (0.07)
Minto	22.90 (0.09)	13.58 (0.08)
Fishing Branch	23.13 (0.09)	13.89 (0.07)
Mean	22.97 (0.05)	13.73 (0.04)
British Columbia		
Mean	22.62 (0.01)	13.42 (0.01)

Developmental Biology

Fecundity and Egg Size

The fecundity-length relationship for 14 female chum salmon is described by

$$F = 0.100\ L^{1.60}$$

where F = number of eggs and L is postorbital-hypural length (mm). Mean fecundity of age 4 females was 2,271 eggs (SD = 208, $n = 7$), and that of age 5 females was 2,451 eggs (SD = 106, $n = 3$).

Mean egg weight of the five Kluane River females used in the study of developmental biology ranged from 145 mg (SD = 6 mg) to 210 mg (SD = 5 mg). Mean diameters ranged from 6.66 mm (SD = 0.21 mm) to 7.25 mm (SD = 0.18 mm). Mean egg size of Yukon River chum salmon is substantially smaller than the mean weight of 290 mg and mean diameter of 8.39 mm for egg size of chum salmon in

TABLE 3.—Mean postorbital-hypural length-at-age (mm) for chum salmon sampled on the spawning grounds during 1984–85. Sample sizes are given in parentheses. The mean length-at-age for British Columbia chum salmon was derived from Beacham and Murray (1987).

	Male age			Female age		
Population	3	4	5	3	4	5
Yukon River						
Kluane	509 (19)	516 (59)	556 (4)	490 (25)	501 (87)	526 (2)
Minto	525 (13)	528 (46)	541 (8)	509 (25)	516 (95)	525 (12)
Fishing Branch	477 (5)	524 (64)	548 (5)	487 (10)	504 (74)	519 (19)
Porcupine		541 (41)	546 (4)	462 (1)	514 (16)	531 (5)
Teslin		521 (17)	521 (14)		492 (19)	506 (14)
Koidern		510 (29)	514 (10)		468 (31)	503 (11)
Mean	510 (37)	524 (256)	531 (45)	497 (61)	505 (322)	515 (63)
British Columbia						
Mean	543 (1974)	595 (3186)	621 (344)	532 (1357)	579 (2879)	605 (255)

TABLE 4.—Mean measurements (mm) for six morphometric characters for chum salmon sampled during 1984. Measurements for each individual were standardized to a postorbital-hypural length of 520 mm. Standard deviations are indicated in parentheses. The size (%) of each standardized character relative to body length is indicated for both Yukon and British Columbia chum salmon. Data for 4,862 male and 4,044 female British Columbia chum salmon were standardized to 600 mm postorbital-hypural length and were derived from Beacham and Murray (1987).

	Kluane	Minto	Fishing Branch	% of length	
				Yukon	B.C.
Males					
Head length	79.4 (4.3)	80.7 (3.3)	81.3 (2.9)	15.48	16.02
Caudal peduncle	39.9 (2.8)	41.5 (2.3)	41.2 (2.5)	7.85	8.37
Anal fin base	67.4 (4.4)	70.0 (3.5)	69.3 (4.4)	13.25	13.68
Anal fin height	57.8 (3.9)	59.5 (3.1)	58.7 (4.5)	11.28	11.65
Dorsal fin base	62.9 (5.6)	66.1 (4.0)	63.9 (4.6)	12.34	13.01
Dorsal fin height	88.1 (6.2)	90.2 (5.4)	92.0 (5.6)	17.33	17.64
Sample size	37	32	39		
Females					
Head length	73.5 (4.3)	74.7 (4.0)	76.3 (3.5)	14.38	14.64
Caudal peduncle	37.7 (3.1)	38.9 (3.3)	39.5 (2.2)	7.44	8.06
Anal fin base	67.8 (5.2)	68.0 (4.8)	68.8 (4.8)	13.12	13.79
Anal fin height	56.0 (4.0)	57.6 (4.8)	58.0 (4.5)	11.00	11.65
Dorsal fin base	58.2 (4.1)	58.4 (4.4)	59.1 (4.4)	11.26	11.79
Dorsal fin height	79.8 (6.5)	82.7 (5.3)	84.4 (5.4)	15.83	16.24
Sample size	63	68	61		

British Columbia (Beacham and Murray 1987).

Survival Rates

Embryo survival rates were lowest at a 4°C incubation temperature and highest at 12°C, with significant differences observed among incubation temperatures ($P < 0.05$) (Table 5). Significant differences were also observed in embryo survival rates among families ($P < 0.0$), but not between replicates within families ($P > 0.10$). An interaction between family and incubation temperature occurred ($P < 0.01$), illustrating that trends in embryo survival with respect to incubation temperature were not the same for all families.

Alevin survival rates were uniformly high (Table 5), with no significant difference observed among temperatures, among families, or between replicates within families. The interaction between family and incubation temperature also occurred for alevin survival rates ($P < 0.05$).

TABLE 5.—Survival rates of embryos and alevins for Kluane River chum salmon maintained at constant water temperatures of 4°, 8°, and 12°C. Time of 50% hatching (days) of the alevins and 50% emergence (days) of the fry is also indicated. *N* is number of fertilized eggs (for embryo survival rates) or alevins hatched (for alevin survival rates). Standard deviations of 50% hatching and emergence times are in parentheses.

Temperature (°C)	*N*	Survival rate	Time to 50% hatching or emergence
Embryos			
4.1 (0.28)	2,172	0.767	113.9 (2.3)
8.0 (0.21)	2,387	0.906	65.7 (0.6)
12.0 (0.35)	2,432	0.955	43.7 (0.9)
Alevins			
4.1 (0.29	1,666	0.975	182.2 (1.9)
8.0 (0.20)	2,162	0.998	111.6 (1.2)
12.0 (0.35)	2,323	0.991	79.6 (1.1)

Hatching and Emergence Time

Warmer water temperatures during incubation enhanced the development rate of Kluane River chum salmon (Table 5). Timings of both alevin hatching and fry emergence at a specific incubation temperature were comparable with that of a British Columbia chum salmon population spawning in late December or early January (Beacham and Murray 1986, 1987), nearly three months later than the spawning time of the Kluane River population.

Alevin and Fry Size

Alevin and fry length and weight were influenced by the water temperature during development. The longest and heaviest alevins and fry were observed at 4°C (Table 6). Significant differences in alevin length and weight were observed among incubation temperatures, among families, and between repli-

cates within families (all $P < 0.05$). Significant interactions between temperature and family were also observed for all alevin size characters (all $P < 0.05$), again illustrating that alevin size characters did not respond consistently among families to changes in incubation temperature.

The effect of different incubation temperatures on fry size characters was similar to that for the alevin size characters. Significant differences in fry length, total weight, and tissue weight were observed among temperatures, among families, and between replicates. The amount of yolk remaining at the time of fry emergence was similar at all incubation temperatures ($P > 0.05$) (Table 6). Interactions between family and incubation temperature were present for all fry size characters (all $P < 0.05$).

TABLE 6.—Fork length, total weight, yolk weight, and tissue weight for Kluane River chum salmon alevins and fry maintained at constant 4°, 8°, and 12°C water temperatures. *N* is the number of alevins and fry measured and weighed for all families combined. Standard deviations are in parentheses.

Temperature (°C)	*N*	Fork length (mm)	Total weight (mg)	Yolk weight (mg)	Tissue weight (mg)
Alevin					
4	150	21.1 (1.4)	222.2 (38.2)	136.9 (19.1)	85.3 (22.4)
8	150	20.8 (0.7)	108.9 (18.9)	106.7 (12.7)	74.2 (8.0)
12	149	20.4 (0.9)	176.6 (20.1)	109.8 (12.9)	66.8 (9.4)
Fry					
4	150	32.3 (1.8)	308.4 (52.9)	30.0 (8.7)	278.4 (51.3)
8	150	31.0 (0.9)	277.5 (27.4)	28.0 (7.2)	249.5 (23.5)
12	150	30.5 (1.1)	277.6 (28.1)	30.7 (6.4)	247.5 (27.2)

Biochemical Genetics

Regional differentiation of allelic frequencies for chum salmon stocks in Alaska and the Yukon Territory was observed. Chum salmon from Alaska generally had a lower frequency of Idh-1^{100} and a higher frequency of Tapep (Lgg)^{75} than those from the Yukon Territory (Table 7). Regional differentiation in allelic frequencies was also observed for the other loci examined. The Delta and Toklat River populations, both tributaries of the Tanana River, had higher frequencies of Idh-3^{100} than all other populations except the Teslin River population. Only one genotypic frequency was not in Hardy-Weinberg equilibrium, that being Pgdh in the Toklat River population. The disequilibrium was due to a heterozygote deficiency.

Variation in allelic frequencies among populations within a region was greater than annual variation in allelic frequencies within a population ($F_{67,48} = 4.00$, $P < 0.01$) (Table 8). Annual stability of allelic frequencies was examined for the loci for which two years of data was available in each population. Of 39 comparisons made, 3 (8%) were significant (Table 8).

Heterozygosity of populations from Alaska was generally higher than that from the Yukon Territory. Mean heterozygosities were 0.156 (SD = 0.009) and 0.138 (SD = 0.019), respectively, for the loci outlined in Table 7. Heterozygosity values are dependent upon the number of polymorphic and monomorphic loci included in the calculations, and thus will vary among studies.

The analysis of genetic distance for all pairwise combinations of the 10 populations sampled ranged from 0.0000 to 0.0072. A dendogram based upon the unweighted pair group mean analysis (UPGMA) illustrated two main clusters of populations (Fig. 2).

FIGURE 2.—Dendogram produced from cluster analysis using Nei's (1978) genetic distance value. Codes are C = Canadian and US = United States.

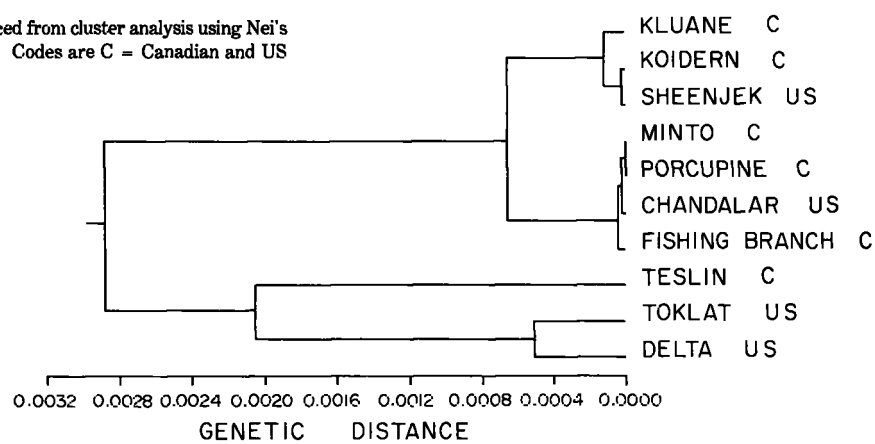

TABLE 7.—Observed allelic frequencies at polymorphic loci for 10 Yukon River drainage and other alleles were assigned numbers

Stock	Year	Idh-1		Idh-3				MdhP	
		N	100	*N*	100	40	85	*N*	100
Kluane	1984	107	1.000	106	0.358	0.585	0.057	107	0.977
	1985	106	1.000	106	0.396	0.552	0.052	106	0.991
	Pooled	213	1.000	212	0.377	0.568	0.054	213	0.984
Minto	1984	130	1.000	130	0.481	0.508	0.012	130	0.904
	1985	114	1.000	114	0.482	0.461	0.057	114	0.899
	Pooled	244	1.000	244	0.482	0.486	0.033	244	0.902
Fishing Branch	1984	126	1.000	126	0.460	0.512	0.028	126	0.944
	1985	99	1.000	98	0.444	0.510	0.046	99	0.914
	Pooled	225	1.000	224	0.453	0.511	0.036	225	0.931
Teslin	1985	90	1.000	90	0.611	0.361	0.028	90	0.889
Koidern	1985	100	1.000	100	0.405	0.570	0.025	100	0.980
Porcupine	1985	81	1.000	81	0.463	0.506	0.031	81	0.938
Toklat	1985	120	0.946	120	0.579	0.350	0.071	120	0.887
	1986	124	0.952	124	0.512	0.399	0.089	124	0.911
	Pooled	244	0.949	244	0.545	0.375	0.080	244	0.900
Delta	1985	146	0.990	145	0.538	0.417	0.045	146	0.877
	1986	147	0.990	146	0.490	0.449	0.062	147	0.884
	Pooled	293	0.990	291	0.514	0.433	0.053	293	0.881
Sheenjek	1985	143	0.993	147	0.398	0.585	0.017	144	0.962
	1986	150	0.987	124	0.415	0.528	0.056	150	0.907
	Pooled	293	0.990	271	0.406	0.559	0.035	294	0.934
Chandalar	1986	147	1.000	143	0.448	0.497	0.056	147	0.939

TABLE 8.—Analysis of heterogeneity of allelic frequencies between countries, among sampled during

Source of variation	Idh-1		Idh-3		MdhP		Mpi	
	df	G	df	G	df	G	df	G
Between countries	1	45.4**	2	12.6**	1	9.6**	1	4.5*
Among populations within countries	8	35.7**	16	77.4**	8	59.2**	8	13.9
Canada	5	0.0	10	34.7**	5	45.2**	5	10.0
United States	3	35.7**	6	42.7**	3	14.0	3	3.9
Between years within populations	6	0.3	12	21.5	6	8.7	6	4.5
Kluane	1	0.0	2	0.6	1	0.6	1	1.3
Minto	1	0.0	2	8.7**	1	0.0	1	0.1
Fishing Branch	1	0.0	2	1.1	1	1.1	1	1.7
Toklat	1	0.0	2	2.3	1	0.5	1	1.2
Delta	1	0.2	2	1.8	1	0.0	1	0.2
Sheenjek	1	0.1	2	7.0	1	6.5**	1	0.0

The Toklat and Delta River populations were distinctive from other populations surveyed. The population from Chandalar River, a tributary of the Porcupine River, was similar to the Porcupine River population (sampled at the Old Crow fishery) and to the Fishing Branch River population, also a tributary of the Porcupine River. The populations from Kluane and Koidern Rivers, tributaries of the White River, were also similar to each other, as well as to the Sheenjek River population in Alaska.

DISCUSSION

Yukon River fall chum salmon undertake the longest freshwater spawning migration of chum salmon in North America and spawn in locations where winter environmental conditions are very severe. They are also relatively abundant, with an average of almost 450,000 chum salmon harvested annually during 1974–83 (Buklis and Barton 1984). Their abundance indicates that they have adapted success-

fall chum salmon populations during 1984–86. The most common allele at a locus was designated 100, according to the mobility relative to that of the 100 allele.

		Mpi		Pgdh		G3pdh-2		Tapep			
Stock	Year	*N*	100	*N*	100	*N*	100	*N*	100	50	75
Kluane	1984	105	0.910	107	0.991	106	0.887				
	1985	106	0.943	105	0.990	104	0.856	106	0.901	0.099	0.000
	Pooled	211	0.927	212	0.991	210	0.871	106	0.901	0.099	0.000
Minto	1984	130	0.923	130	0.962	130	0.888				
	1985	114	0.934	114	0.956	114	0.842	114	0.842	0.158	0.000
	Pooled	244	0.928	244	0.959	244	0.867	114	0.842	0.158	0.000
Fishing Branch	1984	126	0.893	126	0.960	113	0.854				
	1985	97	0.933	99	0.995	96	0.880	99	0.803	0.197	0.000
	Pooled	223	0.910	225	0.976	209	0.866	99	0.803	0.197	0.000
Teslin	1985	90	0.972	90	0.994	89	0.983	90	0.861	0.139	0.000
Koidern	1985	100	0.945	100	1.000	99	0.879	97	0.845	0.155	0.000
Porcupine	1985	79	0.943	81	0.981	75	0.847	80	0.806	0.194	0.000
Toklat	1985	120	0.917	120	0.971	112	0.848	120	0.808	0.158	0.033
	1986	124	0.883	123	0.976	111	0.833	122	0.852	0.119	0.029
	Pooled	244	0.900	243	0.973	223	0.841	242	0.831	0.138	0.031
Delta	1985	141	0.922	146	0.949	134	0.888	146	0.818	0.147	0.034
	1986	147	0.935	147	0.939	104	0.880	142	0.852	0.106	0.042
	Pooled	288	0.929	293	0.944	238	0.884	288	0.835	0.127	0.038
Sheenjek	1985	150	0.913	144	0.972	129	0.876	150	0.847	0.147	0.007
	1986	150	0.913	148	0.973	120	0.879	149	0.822	0.158	0.020
	Pooled	300	0.913	292	0.973	249	0.878	299	0.834	0.152	0.013
Chandalar	1986	145	0.897	147	0.973	85	0.871	145	0.834	0.148	0.017

populations within countries, and between years within populations for Yukon River fall chum salmon 1984–86. $P < 0.01$; $P < 0.05$.

	Pgdh		G3pdh-2		Tapep		Total		Standardized
Source of variation	df	G	df	G	df	G	df	G	F-statistic
Between countries	1	7.9*	1	0.7	2	48.3**	9	129.0**	14.33
Among populations within countries	8	32.0**	8	34.6**	11	20.6*	67	273.4**	4.08
Canada	5	22.6*	5	30.3*	5	10.3	40	153.1**	3.83
United States	3	9.4	3	4.3	6	10.3	27	120.3**	4.46
Between years within populations	6	5.1	6	3.0	6	5.8	48	48.9	1.02
Kluane	1	0.2	1	0.6					
Minto	1	0.0	1	1.9					
Fishing Branch	1	4.8**	1	0.4					
Toklat	1	0.0	1	0.1	2	1.7			
Delta	1	0.1	1	0.0	2	1.8			
Sheenjek	1	0.0	1	0.0	2	2.3			

fully to a long distance freshwater migration and extreme winter conditions.

Several biological characters differ between chum salmon in the Yukon River and in British Columbia. For Yukon River fall chum salmon, approximately equal numbers of salmon mature, on average, at three and five years of age, although there is annual variation (Buklis and Barton 1984). In the Amur River, fall chum salmon mainly mature at four and five years of age (Smirnov 1975). Similar results were recorded in our study. Yukon River chum salmon matured at older ages and at smaller mean lengths-at-age than did chum salmon in British Columbia. A general trend of younger ages at maturity and increased mean lengths-at-age in southern as compared with northern chum salmon populations has been reported by Salo (in press). This trend may be a result of the earlier timing of fry emergence and later timing of adult spawning of more southern populations, allowing more time for

ocean growth, particularly in the year of maturity.

Body shape of Yukon River and British Columbia chum salmon was different, with Yukon River chum salmon having a shorter head, thinner caudal peduncle, and smaller fins than British Columbia chum salmon. This more fusiform body shape is presumably an adaptation to the long migration in fresh water, as selection should result in a body shape that would minimize energy consumption during migration. Morphological differentiation with respect to distance of upstream migration has been reported to occur in other *Oncorhynchus* species (Eniutina 1954; Taylor and McPhail 1985), as well as with respect to river size (Hjort and Schreck 1982; Beacham and Murray 1987).

The mean fecundity of 2,325 eggs per female for Yukon River fall chum salmon reported in our study is similar to other results. Elson (1975) reported mean fecundities of 2,360 eggs and 2,513 eggs per female for Porcupine River chum salmon sampled in 1971 and 1973, respectively. Raymond (1981) reported mean fecundities of Tanana River chum salmon of 2,355 eggs in 1977 and 2,762 eggs in 1978. Fecundities of Yukon River fall chum salmon are less than those reported for many chum salmon stocks in British Columbia (Beacham 1982), and also less than fall chum salmon in the Amur River (3,200 to 4,300 eggs) (Smirnov 1975). Mean egg size of Yukon River fall chum salmon is also less than that of Amur River chum salmon (180 to 300 mg, 6.7 to 9.0 mm diameter) (Smirnov 1975).

The different fecundities and ages at maturity of Yukon River and British Columbia chum salmon present an interesting contrast in life history characters. Yukon River fall chum salmon mature at an average age of 0.28 years older than British Columbia salmon, which means that they incur an additional 5% mortality if the instantaneous mortality rate during the last year of life for chum salmon is 0.013 per month (Ricker 1976). The lower fecundity and older age at maturity of Yukon River salmon indicate that they are not as productive as chum salmon in British Columbia or that mean survival rates of the two groups are not equivalent. Egg-to-fry survival rates for Yukon River chum salmon have been reported as a mean of about 2.5% (Buklis and Barton 1984), whereas those for British Columbia chum salmon average about 10% (Bakkala 1970; Beacham and Starr 1982). If Yukon River chum salmon are as productive as those in British Columbia, then ocean survival rates of Yukon River chum salmon must be higher than those of British Columbia chum salmon.

When incubated under the same water temperatures, Yukon River chum salmon alevins hatch and the fry emerge sooner than most chum salmon populations in British Columbia (Beacham and Murray 1987). The faster development rates presumably occur as a response to lower water temperatures during the winter in the Yukon River tributaries than in rivers in British Columbia. Yukon River chum salmon alevins and fry are shorter and lighter than those from British Columbia (Beacham and Murray 1987), presumably reflective of smaller initial egg size of Yukon River chum salmon. At incubation temperatures of 4°, 8°, and 12°C, maximum alevin and fry size for Yukon River chum salmon was observed at 4°C, but for British Columbia stocks, maximum alevin and fry size was generally observed at 8°C. These results suggest that Yukon River chum salmon are better adapted for development under low water temperatures than are British Columbia chum salmon.

Yukon River chum salmon are generally distinctive in electrophoretic characteristics from chum salmon in Cook Inlet in Alaska (Okazaki 1981) and British Columbia (Okazaki 1981; Beacham et al. 1985, 1987). For example, the allelic frequency of Idh-3^{25} is 0.28 in Queen Charlotte Islands populations and 0.17 in populations in northern British Columbia (Beacham et al. 1987), but this allele was not detected in our study of Yukon River chum salmon. Heterozygosity of Yukon River chum salmon was lower than that observed for British Columbia salmon (the same loci were included in the analysis) (Beacham et al. 1987). Kijima and Fujio (1984) reported that average heterozygosity is related to effective population size in Japanese chum salmon populations, with more abundant populations having increased genetic variance. Abundance of the Yukon River populations examined in our study is unknown, but the catch data suggest that the individual Yukon River populations may not be as abundant as major chum salmon populations in British Columbia.

Allelic frequencies for most salmon populations are reported to show little annual variation (Grant et al. 1980; Utter et al. 1980; Beacham et al. 1985, 1987), allowing for pooling of samples from a particular population over several years. It should thus not be necessary to conduct annual sampling in order to characterize the populations contributing to fisheries. Stock identification based on stable traits, such as allelic frequencies, reduces annual sampling costs for the baseline stocks. This differs from scale analysis, in which variation in the char-

acters used for stock identification makes annual sampling of the baseline stocks necessary (e.g., Wilcock and McBride 1983; Wilcock 1984), and restricts the incorporation of results into management decisions during the fishing season.

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FOOD HABITS AND DAILY RATION OF GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES*, IN THE EASTERN BERING SEA

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ABSTRACT

This study shows that diet of Greenland halibut varies mainly by depth and size, and that size of prey fish increases as the Greenland halibut increases in size. A total of 1,333 Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, stomachs were collected in the eastern Bering Sea from May 1983 to November 1985 and analyzed. Stomach content data were divided into four groups based on sample location (depth). Using length of the sample animals within each depth group, data were further divided into five size groups. Walleye pollock, *Theragra chalcogramma*, was the most important prey (58% by weight of the total stomach content). Squids (mainly *Berryteuthis* sp.) were the second most (20% by weight) important food of Greenland halibut. Zoarcids and some deep-water fishes (e.g., bathylagids, myctophids, macrourids) were also important food for Greenland halibut 30–69 cm long. Euphausiids were only important as food (64% by weight) of the fish <20 cm collected in the continental shelf <200 m deep. Fishes ≥70 cm fed almost exclusively on fish in all depth areas.

Variation in mean stomach content weight throughout the day was used to determine the diel feeding pattern; from this it appears that Greenland halibut is a continuous feeder. Daily rations (% of body weight per day) of Greenland halibut were calculated using an exponential gastric evacuation rate model. Fish ≥70 cm had a higher daily ration value (1.17% of body weight per day) than did those of the two smaller size groups (0.66 and 0.64% of body weight per day for 30–49 and 50–69 cm size groups, respectively).

Greenland halibut (or turbot), *Reinhardtius hippoglossoides*, is an amphiboreal fish, occurring in both the North Atlantic and the North Pacific, but not in the intervening Arctic Ocean (Hubbs and Wilimovsky 1964). Within this range, the species has been most extensively studied in the Atlantic Ocean. In the Pacific Ocean, Greenland halibut has been found from Baja California (Schmidt 1934), Oregon (Niska and Magill 1967), and Vancouver B.C. (Westrheim and Pletcher 1966), through the Bering and Okhotsk Seas (Shmidt 1950), to Honshu Island, Japan (Hart 1973), but the center of abundance is in the eastern Bering Sea area.

Data of the resource assessment surveys (from 1979 to 1985) in the eastern Bering Sea performed by the Northwest and Alaska Fisheries Center (NWAFC), National Marine Fisheries Service (NMFS), show that Greenland halibut ranked between 5th and 12th place in terms of relative abundance (kg/ha) among the groundfish species; however, it is the most abundant species in continental slope areas (Bakkala 1986[2]).

These assessments suggest that Greenland halibut is a key member of the eastern Bering Sea ecosystem. The importance of this species in predator-prey relationships of this ecosystem is poorly understood since little is known about its food habits and food consumption rate. Food habits of Greenland halibut in the North Atlantic have been studied by Bowering and Lilly (1985) and Haug and Gulliksen (1982). In the eastern Bering Sea, Mikawa (1963), Mito (1974), Smith et al. (1978), and Livingston et al. (1986) reported stomach contents analysis of the Greenland halibut, but the sample sizes in these studies were small and the analyses were limited. The objective of this study is to provide a description of the food habits of Greenland halibut in the eastern Bering Sea, including diel, spatial, and seasonal variations in stomach contents; influence of predator size; and daily ration.

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[2]Bakkala, R. G. 1986. Greenland turbot—biological report. Unpubl. manuscr., 21 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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METHODS AND MATERIALS

Sample Collection and Stomach Content Analysis

Stomachs from 1,333 Greenland halibut were collected from May 1983 to November 1985 in the eastern Bering Sea area (Fig. 1) from NMFS research vessels and foreign commercial fishing vessels (through the U.S. Foreign Fisheries Observer Program). A bottom trawl was the only sampling gear used, and trawl samples were taken throughout the day and night. Due to the low abundance of Greenland halibut in the shelf area (<200 m), stomachs were taken from virtually all Greenland halibut encountered in trawl catches. Random size-stratified samples were obtained from the catches in the slope area. Captured fish were checked in the field for signs of regurgitation and were discarded when there was evidence of food items in the mouth or gill plates or of flaccid stomachs. Stomachs from the sampled fish were excised and put into cloth bags with a specimen label containing fork length, sex, and station information, and were preserved in 4% formaldehyde solution. Individual fish weights were not recorded at sea, but were estimated by using the weight-length equation,

$$W(g) = 0.0060717 \times L(\text{cm})^{3.08864}, \qquad (1)$$

estimated from the Greenland halibut data base of the Resource Assessment and Conservation Engineering (RACE[3]) Division of the NWAFC.

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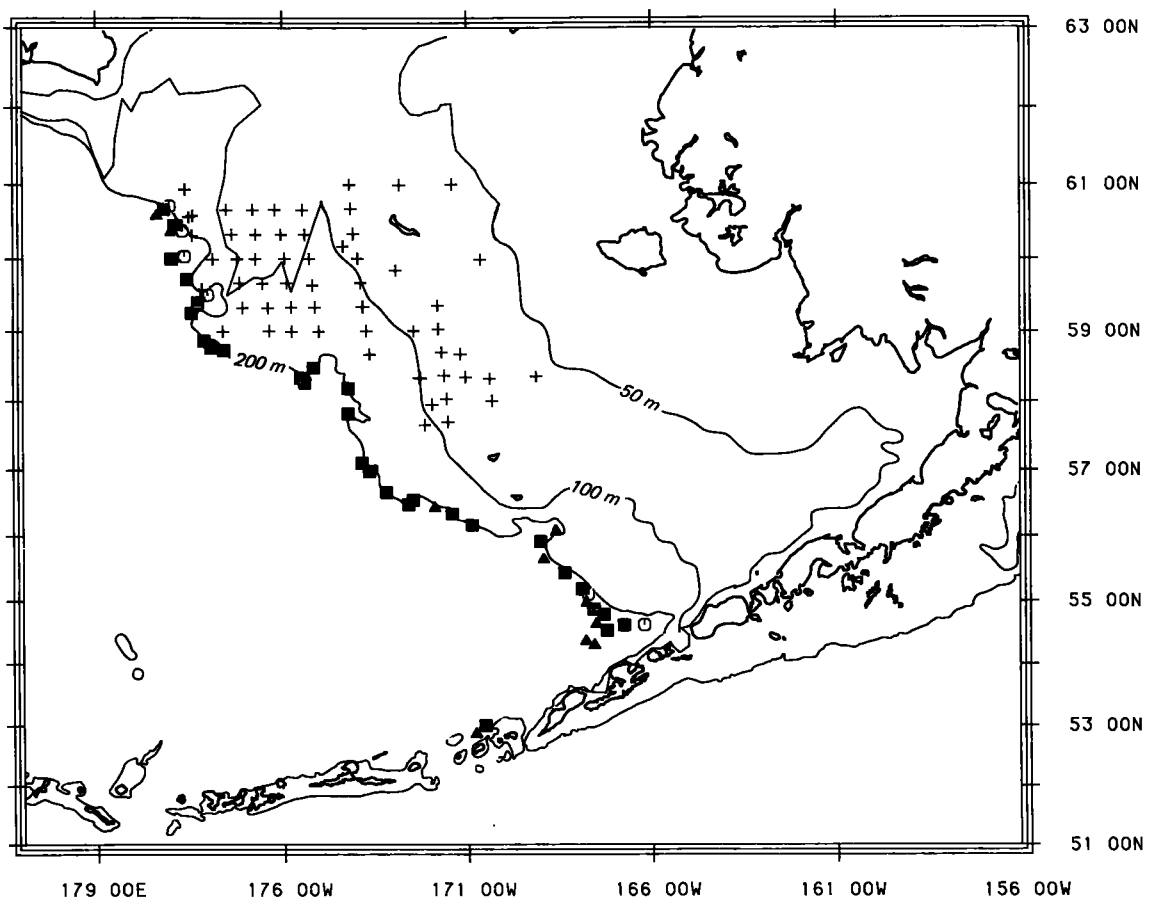

FIGURE 1.—Sampling locations for Greenland halibut in the eastern Bering Sea by four different depth strata, <200 m (+), 200–399 m (O), 400–599 m (■), and ≥600 m (▲).

Stomachs were analyzed individually in the laboratory. Prey items were identified to the lowest possible taxonomic level and counted. Wet weights of the prey items were recorded to the nearest milligram after blotting with paper towels. The fork lengths of prey fish were also measured.

Diet Description

Since the depth distribution of Greenland halibut in this study was broad (from 62 m to 891 m), stomach content data were first subjectively divided by 100 m depth groups. For each 100 m depth class, percent frequency of occurrence (%FO) of prey items, percentage of total stomach content weight (%W) by prey type, and the percentage of total prey number (%*N*) by prey type were calculated by using ECO/INDEX, a computer program for calculating feeding ecology indices (Vodopovich and Hoover 1981). Based on similarities of major prey items (using percent by weight), stomach content data were combined into four depth groups for analysis: Depth 1 (<200 m), Depth 2 (200–399 m), Depth 3 (400–599 m), and Depth 4 (≥600 m).

Within each of the four depth groups, data were subjectively divided by fish length into 10 cm size groups. By comparing percent by weight of the major prey categories (e.g., gadids, squids) for each size group, the fish within each of the four depth groups were finally lumped into five size groups: <20 cm, 20–29 cm, 30–49 cm, 50–69 cm, and ≥70 cm. Seasonal breakdowns of stomach contents by depth and predator size group could not be performed due to insufficient sample sizes.

Diel Feeding Pattern

Because of the small sample size of fish <30 cm long, only data from three size groups (30–49 cm, 50–69 cm, ≥70 cm) were used for diel feeding analysis. For each size group, the stomach content weights as percent of body weight were calculated for each 3-h period of the 24-h day. Any possible seasonal variations of the diel feeding pattern could not be analyzed because of insufficient seasonal samples.

Daily Ration

In this study, daily ration was calculated using Elliott and Persson's (1978) model. The basic assumption of this model are that the rate of gastric evacuation (R) is exponential and temperature dependent. If stomach samples are taken at fixed intervals of t hours, the mean stomach content weight as a percentage of fish weight (S_i) in each interval (i) is calculated for a total of m intervals over the 24-h period. According to Elliott and Persson (1978), the daily ration ($D.R.$) in terms of percentage of body weight is therefore given by

$$D.R. = \frac{Rt}{1 - \exp(-Rt)} \sum_{i=1}^{m} S_i \,(1 - \exp(-Rt))$$

$$= 24\,\bar{S}R \qquad (2)$$

where $\bar{S} = \sum S_i/m$. Elliott (1972) found the general relationship between R and temperature (T) was exponential:

$$R = ae^{bT}. \qquad (3)$$

Based on data presented in the literature for the normal temperature range of both freshwater and marine fishes, Durbin et al. (1983) concluded that the slope (b) is fairly constant for different prey types and fish species (mean = 0.115), while the intercept (a) changes with prey type and can be estimated from gastric evacuation rate experiments. Since there were no gastric evacuation rate data available for Greenland halibut, results of gastric evacuation experiments on walleye pollock, *Theragra chalcogramma*, feeding on juvenile pollock and squid were used (Dwyer et al. 1987). Although walleye pollock is taxonomically very different from Greenland halibut, these two species have some prey in common. In addition, both species are active, off-bottom feeders which could be expected to be more similar in terms of metabolic rates than benthic feeding, small mouth flounders whose food intake has been studied more extensively. The intercept "a" in Equation (2) was 0.0143 for juvenile walleye pollock and 0.0079 for squid. For this study, the intercept for walleye pollock prey was used to calculate daily ration when fish was the main prey (>70% of diet by weight), and the intercept for squid was used when squid was the main prey. If the diet was split evenly between fish and squid prey, daily ration was calculated using both intercept values to obtain a likely range of daily ration values.

Average bottom temperatures for the eastern Bering Sea for this study were estimated from oceanographic data on the Bering Sea (Ingraham

1983[4]). Because of the small differences in temperatures between different seasons (e.g., 2.90°C, 2.47°C, and 2.93°C were the average temperatures for spring, summer, and autumn at locations where fish 30–49 cm were collected), and the lack of samples for fish <30 cm, daily rations were calculated for three size groups (30–49 cm, 50–69 cm, and ≥70 cm) with all seasons combined. Temperatures used for each of the three size-groups were calculated by matching the haul locations of each size group in our study with the long-term monthly mean bottom temperature at those positions and calculating the average bottom temperature.

RESULTS

General Description of Diet

Stomachs from 1,333 Greenland halibut were analyzed; of these, 610 stomachs (46%) were empty. The size of the Greenland halibut ranged from 9 to 99 cm (fork length) with a mean of 56 cm. The sampling depth ranged from 62 to 891 m with most of the samples (55%) collected from the area 400–599 m deep.

Prey consumed included gastropods, cephalopods, crustaceans, ophiuroids, and fish (Table 1). Twelve families of fish and at least 14 different fish species were represented in the stomach contents. Fish dominated the contents in terms of frequency of occurrence, number, and weight; walleye pollock was the most important fish species consumed with respect to all three measures of prey importance. Three genera of squid were consumed (mainly *Berryteuthis* sp.) and were the second most important prey. The importance of the various prey species or groups (e.g., gadids, squids) changes with bottom depth and Greenland halibut size. Those changes will be discussed in the following sections.

Spatial and Size Differences

Depth 1 (<200 m)

Gadids constituted more than 87% by weight of the stomach contents of all but the smallest (<20 cm) size group (Fig. 2A). Euphausiids comprised 64% by weight (54% by number) of the diet of Greenland halibut <20 cm long. In size group 20–29 cm, the percentage by number of euphausiids was still high (52%), but the percentage by weight decreased dramatically to only 2%. Gadids were the dominant prey for size groups larger than 30 cm in Depth 1 in terms of percent of frequency of occurrence, percent of total stomach contents weight, and the percent of prey number. Cephalopods, clupeids, osmerids, stichaeids, myctophids, and macrourids were not important food items at this depth.

Depth 2 (200–399 m)

No Greenland halibut smaller than 30 cm were collected at this depth range. Cephalopods, in terms of the three diet measures shown in Figure 2B, were the dominant food items found in the size groups 30–49 cm and 50–69 cm. On the other hand, gadids were the dominant prey in size group ≥70 cm (Fig. 2B). When all sizes were combined, the cephalopods were more important than gadids (Fig. 2B, lower right); however, when the size groups were separated (Fig. 2B), the different contribution of gadids and cephalopods to different size groups is very clear (cephalopods are most important for fish <70 cm and gadids are important for fish ≥70 cm). Miscellaneous prey fishes found in the entire Depth 2 group included zoarcids, bathylagids, myctophids, and pleuronectids.

Depth 3 (400–599 m)

No stomachs of Greenland halibut smaller than 30 cm were collected in this depth range (Fig. 2C). For Greenland halibut 30–49 cm long, zoarcids (38.6%) were the most important prey item in terms of percentage by weight of the stomach contents, followed by cephalopods (30.7%) and gadids (17%). In terms of percent of prey number, cephalopods comprised 39% of the total prey in this size group, followed by gadids (22%), bathylagids (17.3%), and zoarcids (8.7%). For the size group 50–69 cm, cephalopods, gadids, and zoarcids comprised 61, 21, and 12% by weight of the stomach contents. respectively. Cephalopods also comprised the highest percentage (35%) by the number in this size group. Gadids were the dominant prey of large Greenland halibut (≥70 cm). They comprised 87% by weight, 69% by number, and 82% by frequency of occurrence of the stomach contents of this size group (Fig. 2C). Other prey fishes found in the Depth 3 group included stichaeids, myctophids, cottids, macrourids, cyclopterids, and pleuronectids. For the Depth 3 group (Fig. 2C, lower right), gadids were the domi-

[4]Ingraham, W. J. 1983. Temperature anomalies in the eastern Bering Sea 1953–82. NWAFC Processed Rep. 83-21, 348 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

TABLE 1.—Prey items found in the stomachs of Greenland halibut collected in the eastern Bering Sea during summer 1983 through fall 1985. %FO = percent frequency of occurrence, %*N* = percent by number, %W = percent by weight, t = <0.01% W.

Prey item	%FO	%*N*	%W
Gastropoda			
Buccinum sp.	0.4	0.34	0.14
Cephalopoda	31.9	22.67	20.28
Teuthoidea	30.8	21.98	19.65
Gonatidae	10.5	8.16	11.64
Gonatopsis sp.	1.9	1.20	2.97
Gonatus sp.	0.7	0.60	0.13
Gonatus magister	0.1	0.26	0.09
Berryteuthis sp.	6.4	4.81	6.69
Berryteuthis magister	0.3	0.26	1.03
Unidentified Gonatidae	1.4	1.03	0.73
Unidentified Teuthoidea	20.5	13.82	8.01
Octopoda	0.1	0.09	0.51
Unidentified Cephalopoda	1.0	0.60	0.12
Crustacea	7.8	12.39	0.41
Mysidacea	2.2	1.64	0.01
Gnathopausia gigas	0.7	0.52	t
Holmesiella anomala	1.0	0.77	t
Pseudomma truncatum	0.1	0.09	t
Unidentified Mysidacea	0.4	0.26	t
Cumacea	0.1	0.17	t
Amphipoda	1.2	1.54	t
Gammaridea	1.0	0.77	t
Hyperiidea			
Parathemisto libellula	0.3	0.77	t
Euphausiacea	1.8	4.90	t
Thysanoessa inermis	1.2	3.78	t
Unidentified Euphausiacea	0.6	1.12	t
Decapoda			
Caridea	2.4	3.79	0.15
Pasiphaeidae			
Pasiphaea pacifica	0.1	0.09	t
Hippolytidae	0.4	2.58	0.06
Eualus sp.	0.3	2.06	0.04
Eualus biunguis	0.3	0.52	0.02
Panadalidae	1.2	0.78	0.08
Pandalus sp.	0.8	0.52	0.04
Pandalopsis dispar	0.3	0.17	0.03
Unidentified Pandalidae	0.1	0.09	0.01
Crangonidae			
Crangon communis	0.3	0.17	0.01
Unidentified Caridea	0.3	0.17	t
Reptantia	0.4	0.27	0.25
Anomura			
Paralithodes sp.	0.1	0.09	0.14
Brachyura	0.3	0.18	0.11
Chionoecetes sp.	0.1	0.09	0.08
Chionoecetes opilio	0.1	0.09	0.03
Unidentified Crustacea	0.1	0.09	t
Ophiuroidea	1.1	1.81	t
Ophiurida	1.0	1.72	t
Unidentified Ophiuroidea	0.1	0.09	t
Larvacea Copelata	0.4	0.69	t
Teleostei	71.7	61.36	77.93
Clupeidae			
Clupea pallasii	0.3	0.17	0.74
Osmeridae	0.1	0.09	t
Bathylagidae	7.6	8.24	0.63
Leuroglossus stilbius	0.4	0.43	0.04
Unidentified Bathylagidae	7.2	7.81	0.59
Myctophidae	5.0	6.87	0.71
Stenobrachius leucopsarus	0.1	0.09	t
Unidentified Myctophidae	4.8	6.78	0.71
Gadidae	32.7	26.35	61.08
Theragra chalcogramma	28.2	23.35	58.39
Unidentified Gadidae	4.4	3.00	2.69
Zoarcidae	5.0	4.13	3.51
Lycodes sp.	4.1	3.52	2.95
Lycodes diapterus	0.1	0.09	0.05
Lycodes palearis	0.1	0.09	0.11
Unidentified Zoarcidae	0.6	0.43	0.40
Macrouridae	1.0	1.12	2.00
Coryphaenoides sp.	0.7	0.43	0.39
Coryphaenoides filifer	0.1	0.09	0.04
Unidentified Macrouridae	0.8	0.60	1.57
Icelidae			
Icelus spiniger	0.1	0.09	0.03
Cottidae	0.2	0.18	0.21
Dasycottus setiger	0.1	0.09	0.20
Hemitripterus boline	0.1	0.09	0.01
Cyclopteridae	0.6	0.35	1.73
Aptocyclus ventricosus	0.1	0.09	0.55
Careproctus cypselurus	0.1	0.09	0.82
Unidentified Cyclopteridae	0.3	0.17	0.36
Stichaeidae	0.7	0.43	0.09
Lumpenus maculatus	0.3	0.17	0.04
Unidentified Stichaeidae	0.4	0.26	0.05
Pleuronectidae			
Reinhardtius hippoglossoides	0.6	0.34	1.60
Unidentified Teleostei	20.6	12.88	5.02
Unidentified organic material	0.3	0.17	t
Total number of stomachs	1,333		
Total stomachs with food	723		
Total prey weight (g)	47,713.52		
Total prey number	1,165		

nant prey in the diet due to the consumption of walleye pollock by Greenland halibut ≥70 cm; however, cephalopods and other fishes were more important than gadids for the two smaller size groups.

Depth 4 (≥600 m)

No stomachs were collected for fish smaller than 30 cm in this depth group (Fig. 2D). For size groups 30–49 cm, cephalopods were the dominant prey (56%) of Greenland halibut in terms of percent by weight, followed by bathylagids at 29%. However, the percent of number and the percent of frequency of occurrence of bathylagids (FOG in Figure 2D, upper left) were higher than those of the cephalopods. The stomach contents (by weight) of Greenland halibut 50–69 cm long was composed of 57% cephalopods, 22% macrourids, 12% bathylagids, 4%

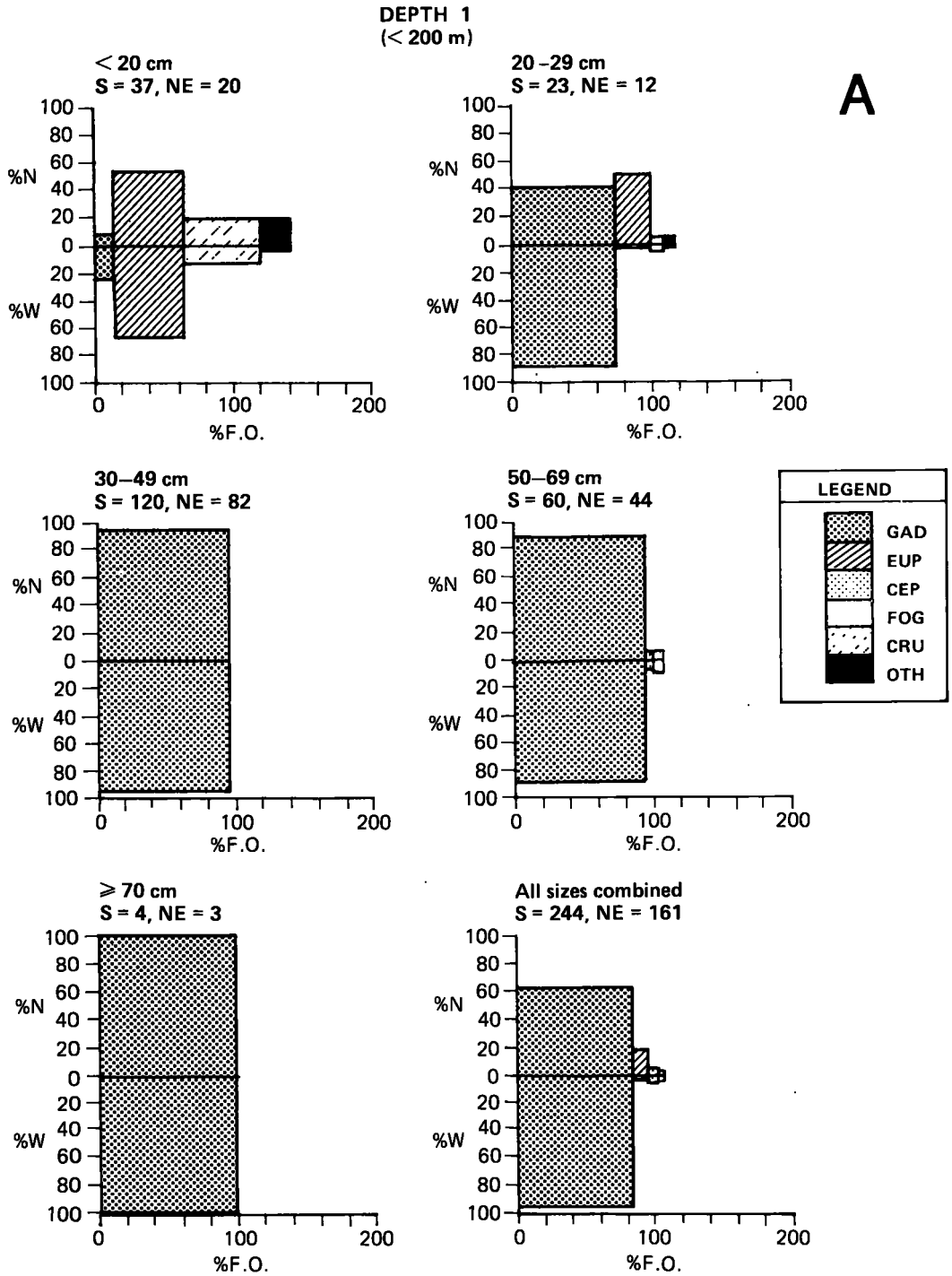

FIGURE 2.—Percent of frequency of occurrence (%FO), percent of prey number (%*N*), and percent of stomach content weight (%W) of major prey items in the stomach contents of Greenland halibut (by depth and by size). S, total number of stomachs; NE, nonempties; %FO, GAD, Gadids; EUP, Euphausiids; CEP, Cephalopod; FOG, Fish other than gadids; CRU, Crustacean; OTH, Others. A) Depth 1.

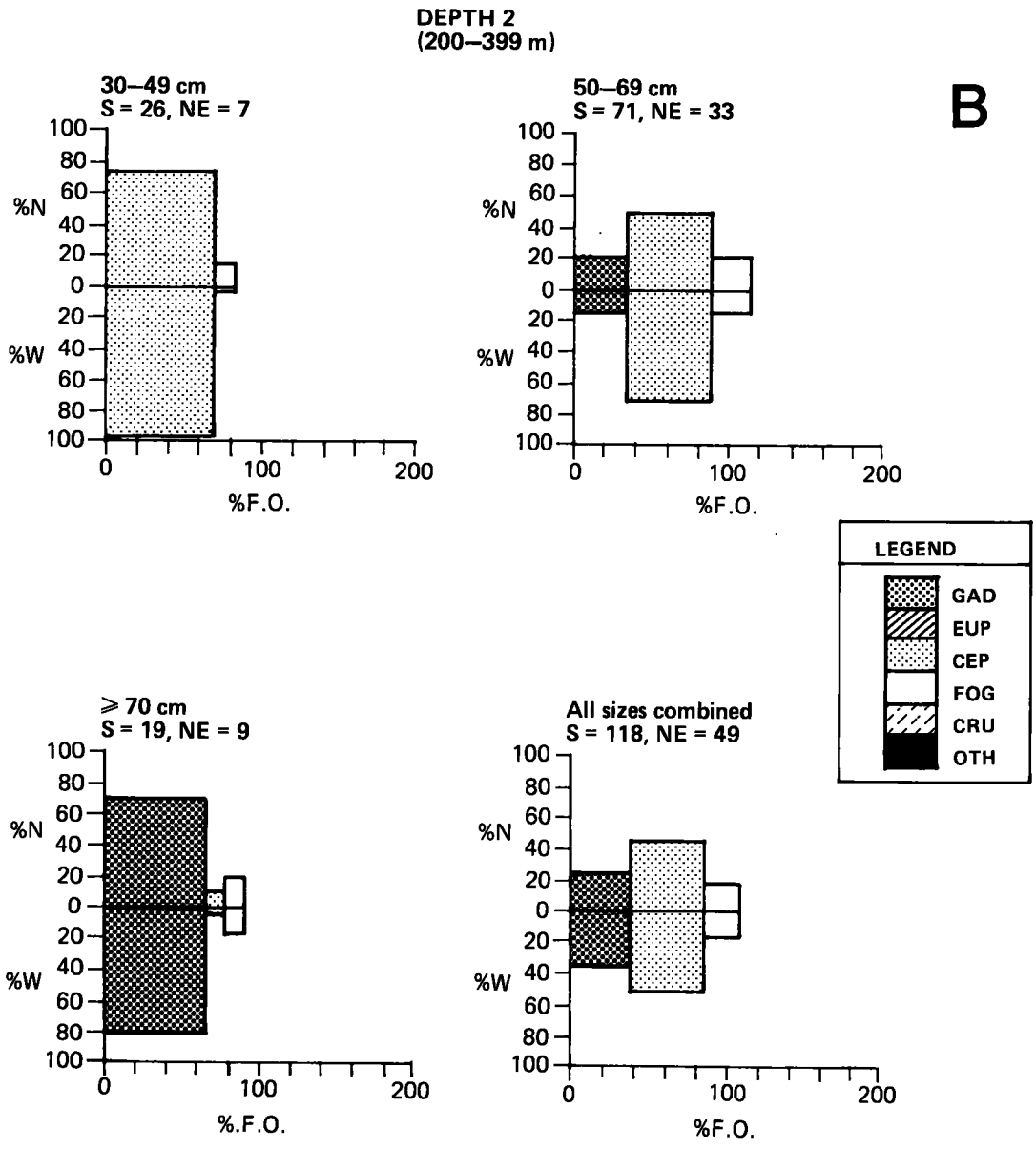

FIGURE 2.—*Continued.*—B) Depth 2.

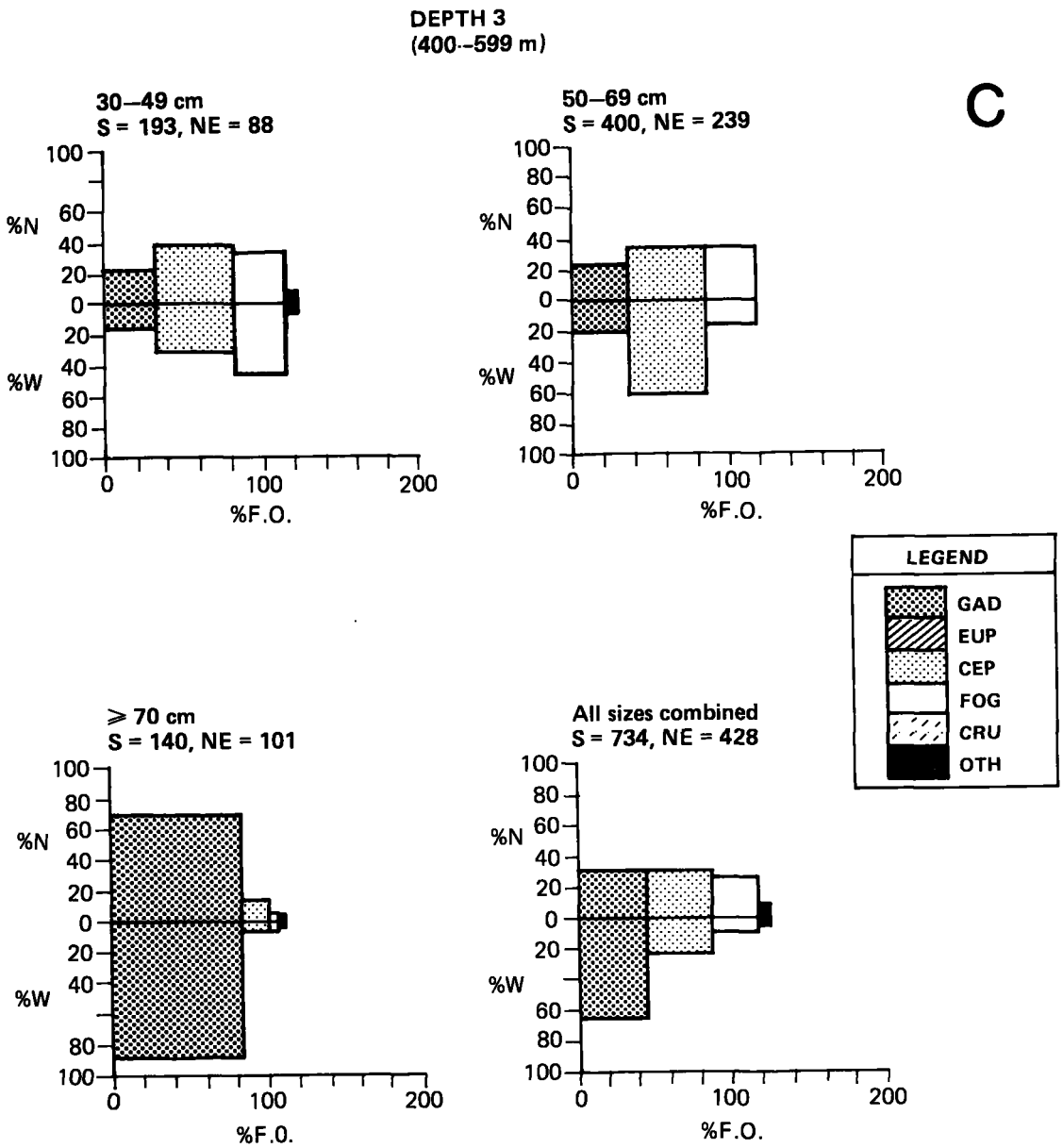

FIGURE 2.—*Continued.*—C) Depth 3.

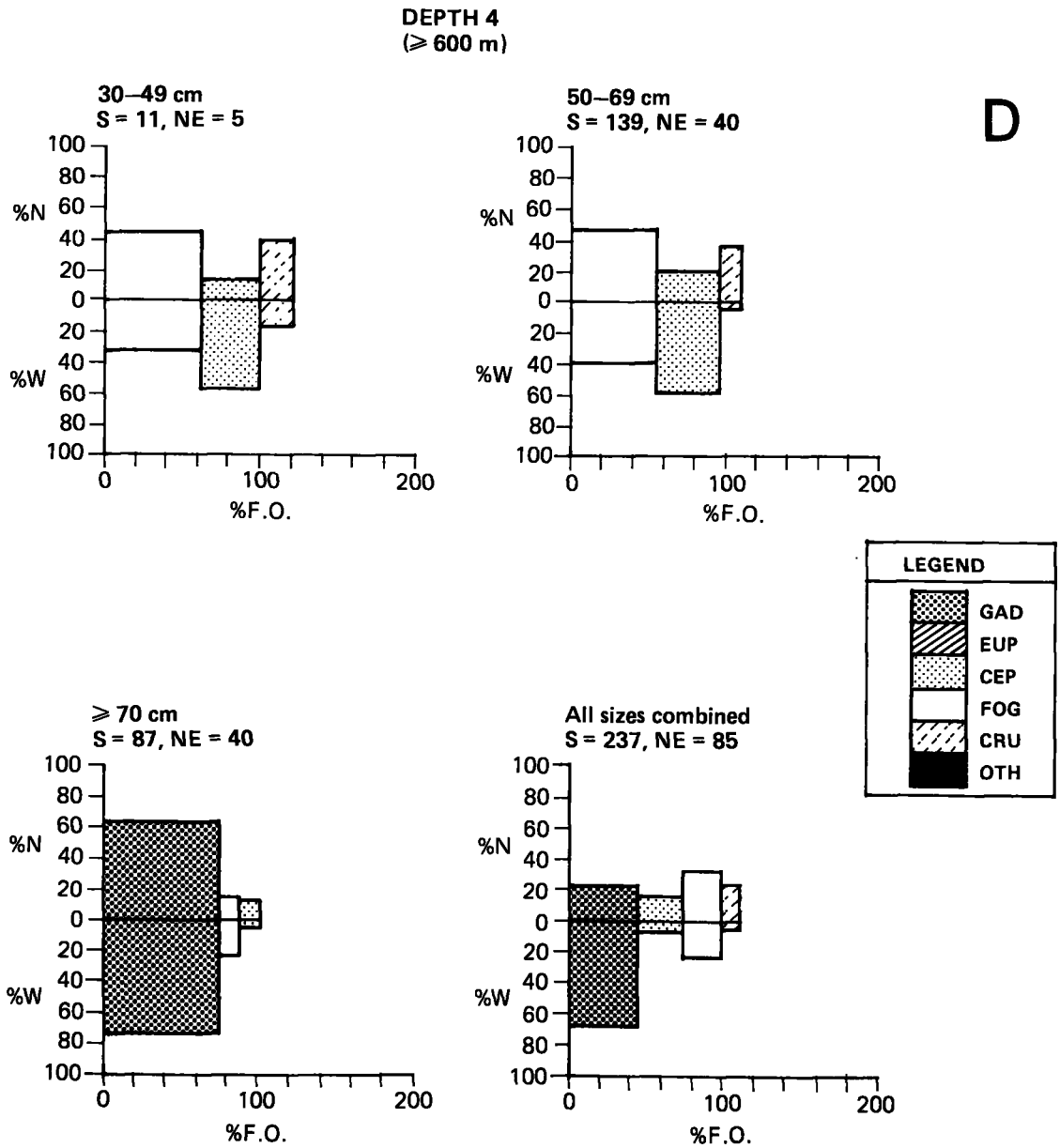

FIGURE 2.—*Continued.*—D) Depth 4.

myctophids, and 0.6% stichaeids. In terms of percent by number and the percent of frequency of occurrence, the fishes other than gadids (FOG in Figure 2D) were more important than the cephalopods. No gadids were found in either the 30–49 cm group or the 50–69 cm group of fishes; however, they were the dominant prey (75% by weight, 64% by number, and 73% by frequency of occurrence) of Greenland halibut ≥70 cm (Fig. 2D, lower left) as in the other three depth groups (Fig. 2A,B,C, lower left). Other food in this size group included macrourids, cyclopterids, and pleuronectids. Even though gadids did not occur in the two smaller size groups, they were important in the Depth 4 group as a whole (Fig. 2D, lower right).

Trends in Fish Consumption

The size of the walleye pollock consumed by Greenland halibut increased dramatically with predator size (Fig. 3). The relationship appears linear with $r^2 = 0.835$. Based on the age-length key for walleye pollock (Halliday and Umeda 1986), the walleye pollock eaten by Greenland halibut were approximately age 0 and age 1 for smaller size fish (<50 cm), age 1 and age 2 for medium size fish (50–69 cm), and age 3 and age 4 for the fish ≥70 cm (Fig. 4).

The importance of prey fishes in the diet of Greenland halibut appears to be depth related (Table 2). Clupeids disappear from the diet in waters ≥200 m deep, while gadids are important in all depths but occur most frquently (85%FO), and comprise most of the diet both in number and weight (65% and 93%, respectively), in the area <200 m deep. Zoarcids appear in stomachs only in the area 200–600 m deep, and bathylagids start appearing at 200–399 m and increase in importance as the water depth increases. Myctophids seem to be more important in the area 400–599 m than in the other depths,

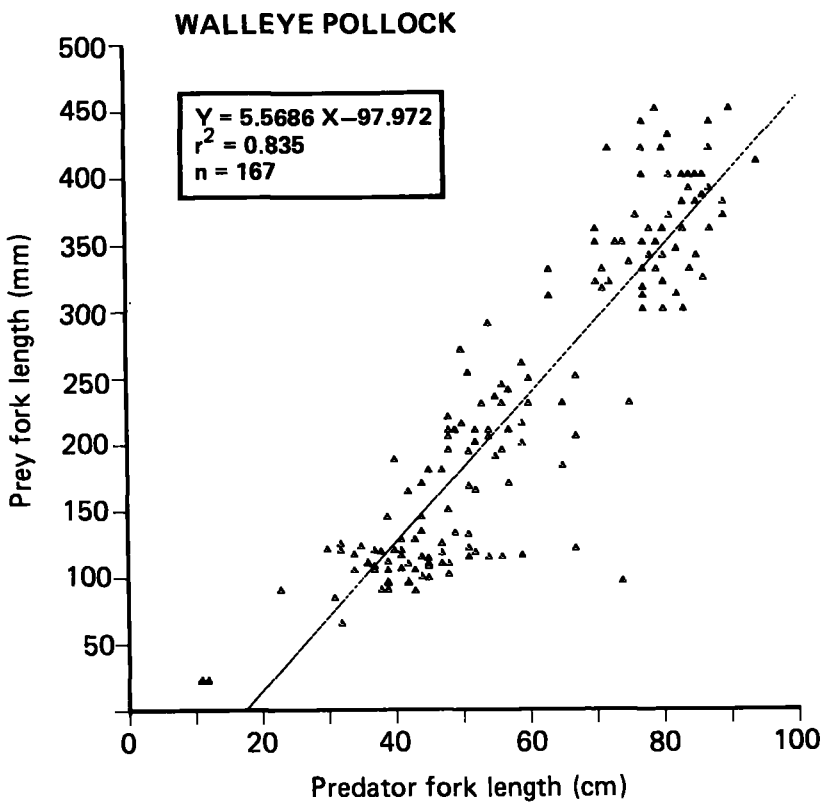

FIGURE 3.—Scatter plot of the fork length of walleye pollock that were consumed by Greenland halibut of different sizes in the eastern Bering Sea.

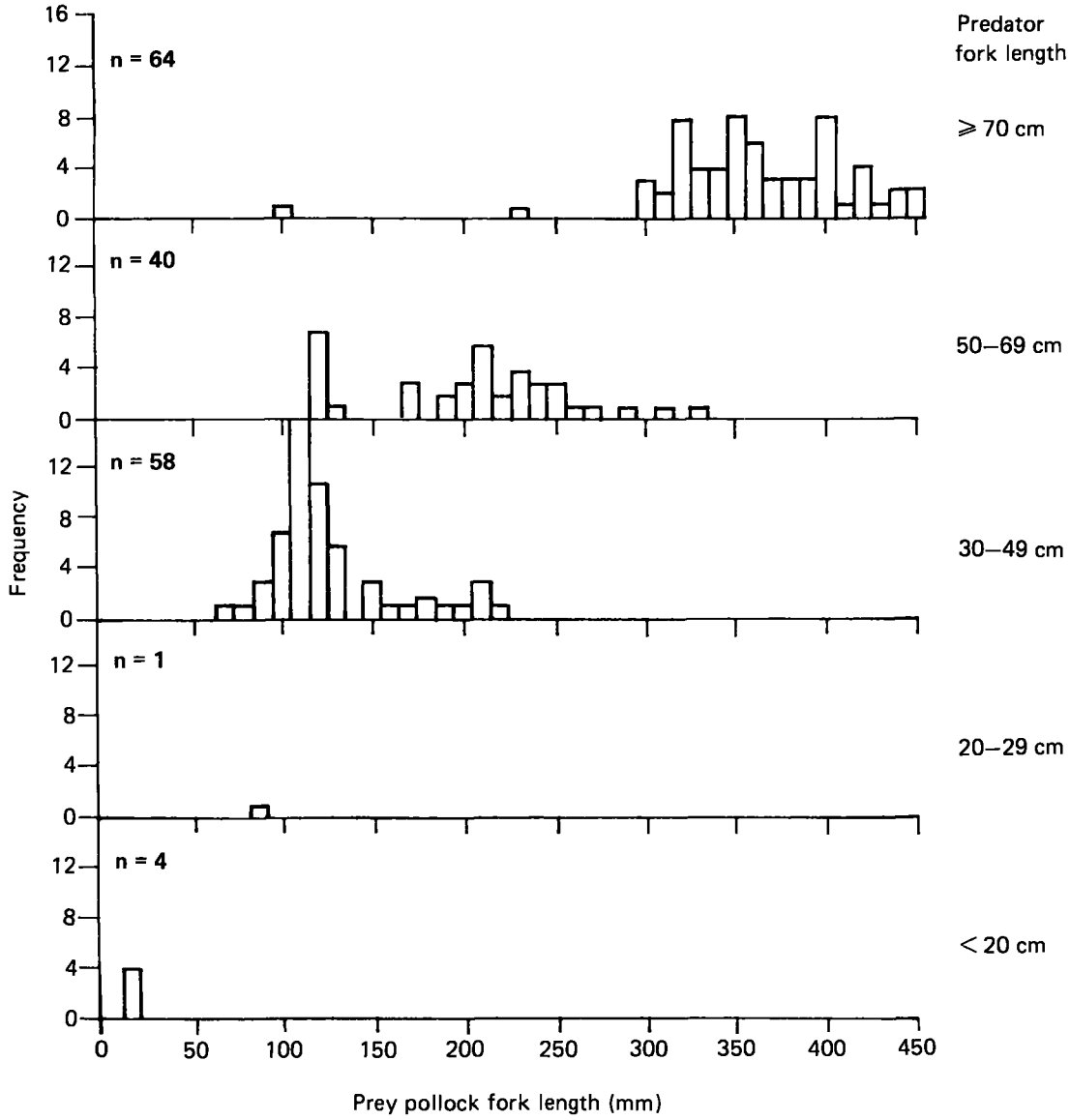

FIGURE 4.—Length-frequency distributions of walleye pollock consumed by Greenland halibut in the eastern Bering Sea.

while macrourids are important prey in even deeper waters (⩾600 m).

Trends in Stomach Fullness

Fewer empty stomachs were found in summer than in spring and autumn except in the ⩾70 cm size group (Fig. 5). The occurrence of empty stomachs for all size groups was about 35% in summer and 50% in autumn. In spring, samples from the 30–49 cm size group had the greatest percentage of empty stomachs (about 70%), followed by size groups 50–69 cm (about 58%) and ⩾70 cm (about 12%).

There were no apparent diel trends in stomach content weight in this study (Fig. 6). The stomach content weight (expressed as percentage of body weight) for large fish (⩾70 cm) was fairly constant except for the 0900–1200 h time period. The

TABLE 2.—Importance of the prey fish by depth found in the stomachs of Greenland halibut collected from the eastern Bering Sea. %FO = percent frequency of occurrence, %*N* = percent by number, %W = percent by weight.

	Depth 1 (<200 m)			Depth 2 (200–399 m)			Depth 3 (400–599 m)			Depth 4 (≥600 m)		
Prey fish	%FO	%*N*	%W	%FO	%*N*	%W	%FO	%*N*	%W	%FO	%*N*	%W
Clupeidae	0.6	0.3	2.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Osmeridae	0.6	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Stichaeidae	1.2	0.7	0.4	0.0	0.0	0.0	0.5	0.3	0.1	1.2	0.7	0.1
Gadidae	85.1	64.9	92.7	36.7	26.5	36.2	45.3	31.4	64.4	42.4	25.2	67.9
Zoarcidae	0.0	0.0	0.0	8.2	8.8	7.0	7.4	6.5	4.8	0.0	0.0	0.0
Bathylagidae	0.0	0.0	0.0	6.1	5.9	0.1	9.8	9.4	0.5	11.8	21.7	2.1
Myctophidae	0.6	0.3	0.1	4.1	4.4	0.2	7.2	11.1	1.3	2.4	2.8	0.4
Cottoidei	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.5	0.4	0.0	0.0	0.0
Macrouridae	0.6	0.3	0.5	0.0	0.0	0.0	0.9	0.8	1.1	8.3	4.9	9.4
Cyclopteridae	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.5	1.4	1.2	0.7	6.0
Pleuronectidae	0.0	0.0	0.0	2.0	1.5	6.0	0.2	0.2	0.9	2.4	1.4	4.7

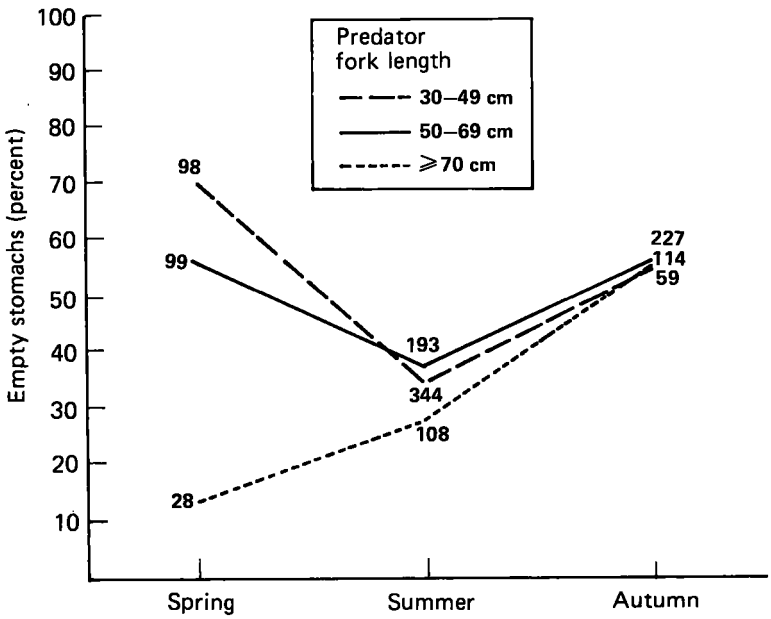

FIGURE 5.—Percent of empty stomachs by season and Greenland halibut size. (Numbers are sample sizes.)

stomach content weight of the fish 50–69 cm was also fairly constant although much less than in the larger fish. Although a midday drop in stomach content weight occurred in the two larger size groups, stomach content weight for the smallest size group appeared to steadily increase from 0100 h to 1200 h. The stomach content weight was highest but most variable in size group 30–49 cm during the 1500-1800 h time period.

Daily Ration

The mean stomach content weight and the daily ration varied among three size groups of Greenland halibut (Table 3). By percent body weight, the mean stomach content weight for 30–49 cm and 50–69 cm size groups were 1.4% and 1.3% respectively. Fish ≥70 cm had the greatest mean stomach content weight (2.4% of body weight). Since gastric evacu-

TABLE 3.—Daily ration (*D.R.*) and mean stomach content weight (%BW ± SE) of Greenland halibut during each 3-h period. BW = body weight; *N* = No. of stomachs (including empty stomachs).

Size class (Temperature)	Time period	*N*	Mean stomach content weight (%BW ± SE)
30–49 cm	2400–0300	64	0.4700 ± 0.1772
(2.64°C)	0300–0600	21	0.9537 ± 0.4470
fish as prey	0600–0900	44	1.1542 ± 0.2926
a = 0.0143	0900–1200	59	1.7173 ± 0.3097
R = 0.0194	1200–1500	27	1.8937 ± 0.5661
D.R. = 0.6644	1500–1800	52	2.5844 ± 1.4731
	1800–2100	49	0.7300 ± 0.2425
squid as prey	2100–2400	34	1.9124 ± 0.3710
a = 0.0079			
R = 0.0107			$\bar{S}$ = 1.4270
D.R. = 0.3665			
50–69 cm	2400–0300	49	0.9141 ± 0.1306
(2.93°C)	0300–0600	78	1.5944 ± 0.3292
fish as prey	0600–0900	108	1.6596 ± 0.3011
a = 0.0143	0900–1200	70	1.0256 ± 0.2566
R = 0.0200	1200–1500	70	1.6406 ± 0.2736
D.R. = 0.6380	1500–1800	87	0.8967 ± 0.2340
	1800–2100	97	1.5372 ± 0.3077
squid as prey	2100–2400	111	1.3652 ± 0.2646
a = 0.0079			
R = 0.0111			$\bar{S}$ = 1.3292
D.R. = 0.3541			
⩾70 cm	2400–0300	25	2.8888 ± 0.6365
(2.96°C)	0300–0600	22	2.4635 ± 0.6325
fish as prey	0600–0900	28	3.2101 ± 0.6714
a = 0.0143	0900–1200	21	1.0156 ± 0.3308
R = 0.0201	1200–1500	40	2.8228 ± 0.5439
D.R. = 1.1712	1500–1800	40	1.7294 ± 0.4454
	1800–2100	41	2.5454 ± 0.6559
	2100–2400	33	2.7468 ± 0.4782
			$\bar{S}$ = 2.4272

ation rate (R) is affected by prey type, the constant a, used to calculate R for each size group, was determined by the percentage by weight of the main prey items (fish or squid). In size group 30–49 cm, where fish constituted 72% and squid constituted 25% by weight of the diet, both a = 0.0143 (fish as prey) and a = 0.0079 (squid as prey) were used for calculating R. For size group 50–69 cm, fish constituted 47% of the diet and squid 52%, so gastric evacuation rates were also calculated by using both a = 0.0143 and a = 0.0079. For size group ⩾70 cm, prey fish comprised 94% of the diet, and a = 0.0143 was used for calculating the gastric evacuation rate.

Large Greenland halibut (⩾70 cm) had the highest daily ration value (1.17%), measured as percentage of body weight per day (BWD), followed by the size group 30–49 cm (0.66% BWD). The 50–59 cm size group had the lowest daily ration value, 0.64% BWD

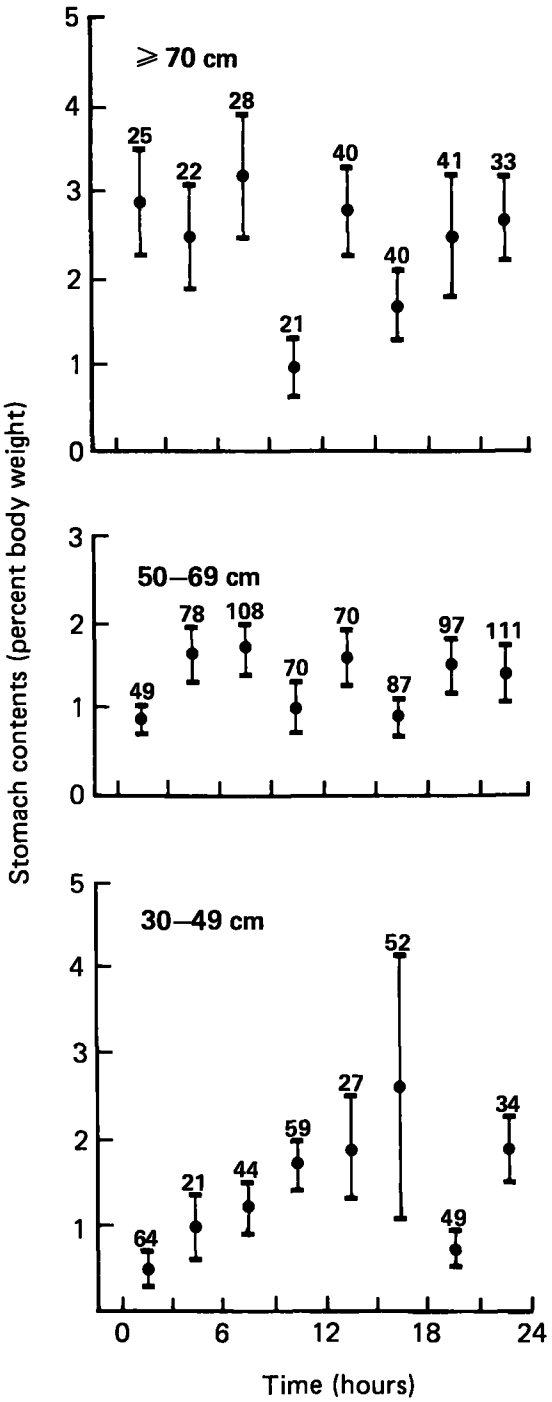

FIGURE 6.—Diel changes in mean stomach content weight (%BW ± SE) in the stomachs of three different size groups of Greenland halibut (the number above each bar was the sample size).

for fish prey and 0.35% BWD for squid prey. Since, fish and squid each constituted about one half of the stomach contents by weight in this size group, the actual daily ration lies within the range of the two values, 0.64% and 0.35%.

DISCUSSION

This study demonstrates size-dependent prey preference by Greenland halibut; halibut <20 cm fed primarily on euphausiids whereas those ≥20 cm were largely fish and squid eaters. It is not surprising to find that walleye pollock was the dominant prey (Table 1) of Greenland halibut because the estimated biomass of walleye pollock in the Bering Sea area is about 10,000,000 metric tons (Bakkala and Wespestad 1983). Livingston et al. (1985[5], 1986) noted that walleye pollock is a major food source not only for marine birds, marine mammals, and man, but also serves as a major food source for dominant components of the eastern Bering Sea groundfish complex. Other studies have also shown the importance of walleye pollock as food of Greenland halibut (Moiseev 1953; Mito 1974; Smith et al. 1978) in the eastern Bering Sea.

In this study, large Greenland halibut (≥70 cm) ate fish almost exclusively. Bowering and Lilly (1985) found that 65–69 cm was the length at which Greenland halibut in the northwestern Atlantic began to switch from smaller pelagic fish (*Mallotus villosus*) to larger groundfish (*Gadus morhua, Sebastes* sp., Anarhichadidae, Pleuronectidae, Zoarcidae) as food. Mikawa (1963) noted increased piscivory with size in Greenland halibut sampled in several areas of the North Pacific. Mito (1974) also showed the same trend; he found that 65–90 cm Greenland halibut ate 20–40 cm long walleye pollock. These observations suggest that large Greenland halibut (≥70 cm) feed on larger sized groundfish which may be lower in the water column whereas the smaller Greenland halibut (<70 cm) feed on smaller sized pelagic fish in the upper water column.

Shuntov (1970) and Mikawa (1963) noted seasonal depth migrations for Greenland halibut and interpreted the summer movement into shallower waters as a feeding migration related to migrations of walleye pollock. Based on the size distribution of walleye pollock in midwater trawl catches near the Pribilof Islands and westward over the Aleutian Basin, Livingston and Dwyer (1986) found that small (age 0) pollock occurred in near-slope and shelf areas, medium (age 1) pollock in shelf areas, while larger (>1 year old) pollock occurred in all areas during summer. Therefore, it can be concluded that in the slope area, where juvenile walleye pollock (age 0 and 1) of the appropriate size for smaller Greenland halibut were not available, the smaller sized (30–69 cm) Greenland halibut ate the available prey, cephalopods and deep-water fishes, while the larger ones (≥70 cm) consumed mostly larger walleye pollock (≥30 cm) and other fish regardless of depth or season.

No clear diel feeding trends were found. The lack of trends may be related to the large variations of the time of sunrise and sunset in different seasons in the Bering Sea. Other studies have varied findings. Mito (1974) reported that Greenland halibut fed primarily from sunset to midnight based on limited sample sizes (six specimens in some time periods). Shuntov (1970) showed that this species fed continuously in the Okhotsk Sea, although feeding was somewhat higher during the night. By comparing day and night catch rates, Chumakov (1969) concluded that Greenland halibut (in the Iceland area) made daily vertical migrations (staying close to the bottom during the day and moving up in the water column at night). However, he did not correlate this behavior with diel feeding. Thus, the literature and this study show no definite diel feeding trend in Greenland halibut.

Daily Ration

Daily ration calculations were based on the evacuation rate of one prey item (pollock or squid) using Elliott and Persson's (1978) model. Other authors (Durbin et al. 1983; Dwyer 1984) have calculated total daily ration by adding up the separate daily rations of the different prey items. Persson (1984) demonstrated that the evacuation of a specific food item can be dependent on the ingestion of other food items. Therefore, it may be erroneous to apply the food consumption model to estimate the consumption of individual prey types separately. Persson (1984) suggested that the only practical solution to calculate the daily rations of different prey items is to calculate the mean weight of each food item remaining in the digestive tract over 24 hours and multiply the fraction it constitutes of the total mean content with the total daily ration. This is necessary

[5]Livingston, P. A., M. S. Yang, and D. Wencker. 1985. The importance of juvenile pollock in the diet of key fish species in the eastern Bering Sea. Unpubl. manuscr., 19 p. Presented as the workshop on comparative biology, assessment, and management of gadoids from the North Pacific and Atlantic Oceans, 24–28 June 1985. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115.

since the complexity of feeding and evacuation patterns in field populations of fish makes it impossible to estimate the consumption and evacuation of different food items ingested at different times.

Bowering and Lilly (1985) estimated the consumption rate of capelin, *Mallotus villosus*, by Greenland halibut in the northwestern Atlantic, using estimates of gastric evacuation rate for Atlantic cod, *Gadus morhua*, on capelin from Minet and Perodou's (1978) study. Assuming a linear gastric evacuation model, they found the time for Greenland halibut to complete digestion of capelin at 2°–3°C was 3–5 days. By using the gastric evacuation rate calculated from this study, the time needed by large Greenland halibut (≥70 cm) to evacuate 99% of a pollock meal at 3°C was 4.2 days, a value very similar to Bowering and Lilly's (1985) estimate.

Livingston and Dwyer (1986[6]) calculated an average daily ration for arrowtooth flounder of 0.62% of body weight per day. This value is close to the daily ration values calculated from this study. Since Greenland halibut and arrowtooth flounder are ecologically and morphologically similar species, it is not surprising to find their daily ration needs are similar.

Huebner and Langton (1982) performed a gastric evacuation study on winter flounder, *Pseudopleuronectes americanus*. They used squid as food for fish 10–40 cm at 5.5°–7.0°C to get a gastric evacuation rate of 0.079/h and calculated daily ration in the range of 1.8–2.4% BWD. Compared to these values, the daily ration of Greenland halibut calculated in this study is low, possibly due to the lower temperatures in this study.

Greenland halibut ≥70 cm apparently ate a higher daily ration (1.17% of body weight per day) than did those <70 cm (0.66% and 0.64% BWD for size group 30–49 cm and 50–69 cm, respectively). Flowerdew and Grove (1979) studied the effects of body weight and meal size on gastric emptying time in the turbot, *Scophthalmus maximus*. Their results showed that large fish emptied a meal of a given size from the stomach at a faster rate than small fish, and large meals in a given fish were processed at faster rate than small meals. Dwyer (1984) also found a higher daily ration value for larger walleye pollock in the eastern Bering Sea. However, Windell (1978) stated that small fish generally consume proportionately more food per unit weight, and some studies showed this trend; Daan (1973) used a prey size dependent evacuation model and found that ration decreased with increasing fish size for North Sea Atlantic cod. Huebner and Langton (1982) calculated daily ration of winter flounder and found the largest fish (>300 g) had the smallest ration. Other studies (Elliott 1972; Hofer et al. 1982) showed that predator size and meal size have little or no effects on gastric evacuation rate. Durbin and Durbin (1980) concluded from an extensive review of daily ration studies that particle size and meal size relationships on gastric evacuation rates deserve further study. Since the ≥70 cm Greenland halibut in this study, which had the highest daily ration, also consumed much larger walleye pollock than the other predator size groups, a particle size interaction with gastric evacuation rate seems a likely avenue for further research.

[6]Livingston, P. A., and D. A. Dwyer. 1986. Food web interactions of key predatory fish with northern fur seal, *Callorhinus ursinus*, in the eastern Bering Sea during summer 1985. *In* T. R. Loughlin and P. A. Livingston (editors), Summary of joint research on the diets of northern fur seals and fish in the Bering Sea during 1985, p. 57–92. NWAFC 86-19. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115.

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ASPECTS OF THE BIOLOGY OF TWO SCYLIORHINID SHARKS, *APRISTURUS BRUNNEUS* AND *PARMATURUS XANIURUS*, FROM THE UPPER CONTINENTAL SLOPE OFF SOUTHERN CALIFORNIA

JEFFREY N. CROSS[1]

ABSTRACT

The distribution, abundance, reproductive cycle, and food habits of two scyliorhinid sharks are discussed. Catsharks occurred on 87% of 71 longline sets and in 6% of 48 trawls. Longline catches were stratified by habitat into banks (hard substrate) and mud (soft substrate). *Apristurus brunneus* occurred more frequently on mud sets than on bank sets, but its abundance was similar in both habitats. *Parmaturus xaniurus* occurred equally frequently on mud and bank sets, but it was more abundant on bank sets. Catches of both species consisted of adults and adolescents; juveniles were rare or absent. Historical collections suggest that juveniles are mesopelagic.

Male *P. xaniurus* matured at a smaller size than male *A. brunneus*. Females of both species matured at about the same size and fecundity increased with female size. The proportion of body weight devoted to gonads and maximum oocyte size were greater among *P. xaniurus*, but fecundity and the proportion of females carrying egg cases were greater among *A. brunneus*. Seasonal changes in gonadal development were not well defined for either species. Members of both populations may have been reproductively active throughout the year.

The diets of both species comprised, in order of importance, crustaceans, teleosts, and squids. Most prey consumed were pelagic; however, it is not known where in the water column the catsharks obtained their prey.

The Scyliorhinidae is the largest family of living sharks with about 94 valid species (Nelson 1984). Commonly known as catsharks, they occur worldwide from tropical to cold-temperate and arctic waters from the intertidal to depths greater than 2,000 m. Little is known about the biology of most scyliorhinid sharks despite their abundance and widespread distribution (Springer 1979; Compagno 1984).

Apristurus brunneus Gilbert, the brown catshark, occurs in the eastern Pacific Ocean from northern British Columbia, Canada, to northern Baja California, Mexico, and perhaps south to Central America and Peru. It is common on the outer continental shelf and upper slope off British Columbia, Washington, and northern California (Springer 1979) but is considered uncommon off central and southern California (Miller and Lea 1972). DeLacy and Chapman (1935) and Cox (1963) described its egg case. Jones and Geen (1977) made observations on its distribution, reproduction, and food habits in British Columbia waters.

Parmaturus xaniurus Gilbert, the filetail catshark, occurs in the eastern Pacific Ocean from central California to the Gulf of California, Mexico. It is fairly common on the outer continental shelf and upper slope (Compagno 1984). Cox (1963) described its egg case. Lee (1969) reported that juveniles were captured by midwater nets in the Santa Barbara basin off southern California. Springer (1979) reported that *P. xaniurus* were observed eating moribund lanternfishes (Myctophidae) at the bottom of the oxygen-poor Santa Barbara Basin.

The objective of this study was to increase the knowledge of the life histories of *A. brunneus* and *P. xaniurus* by analyzing data on the distribution, abundance, reproduction, and food habits of these species collected during a survey of the fishes of the upper continental slope off southern California (Cross 1987).

MATERIALS AND METHODS

Fishes occurring on or near the bottom between 290 and 625 m were collected by otter trawl and longline. Forty-eight trawls were made between November 1981 and August 1983 (Fig. 1). A single warp semiballoon trawl with 7.6 m headrope, 8.8 m

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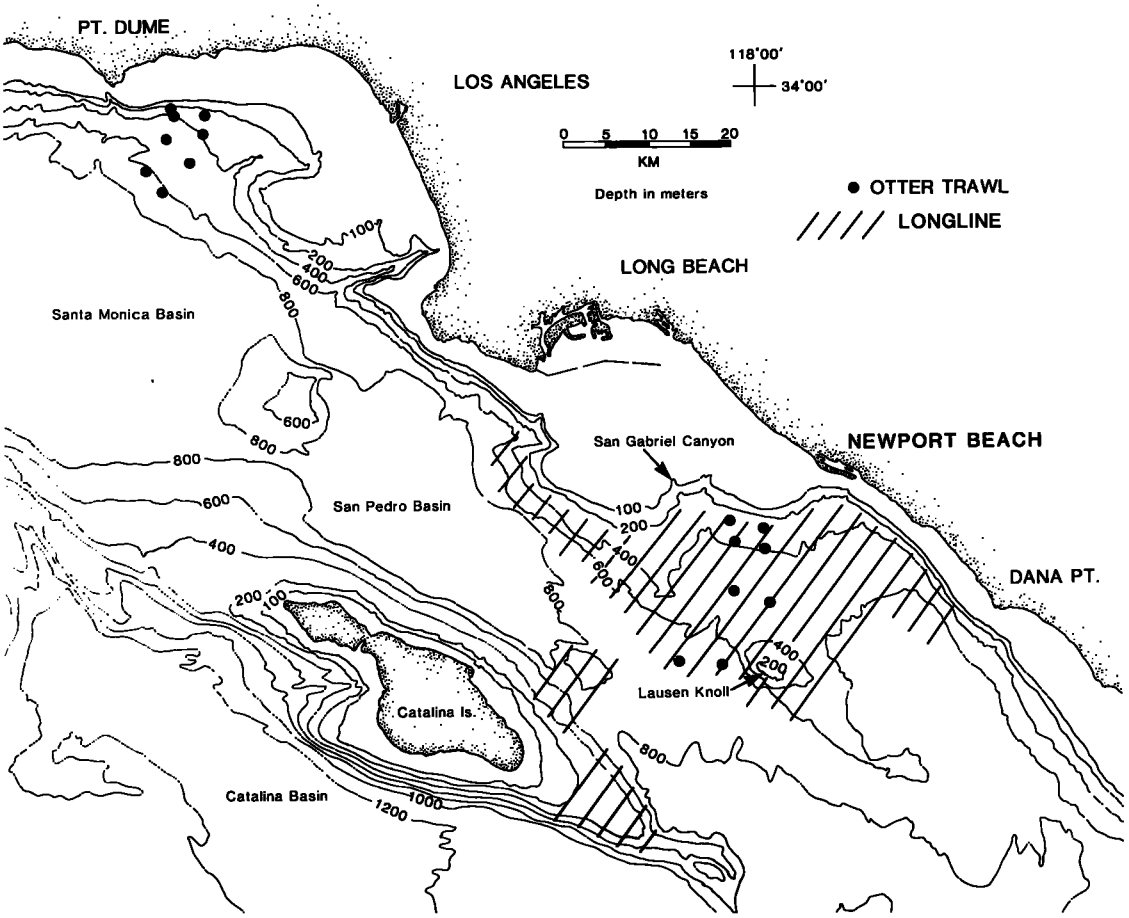

FIGURE 1.—Map of the study area.

footrope, 4.1 cm (stretched) body mesh, and 1.3 cm (stretched) cod end liner was towed along an isobath at approximately 2.5 knots for 10 minutes.

Seventy-one trips were made with commercial longline fishermen between June 1983 and November 1984 (Fig. 1). A unit (tub) of longline gear consisted of about 650 m of groundline bearing approximately 600 hooks (4/0 and 5/0 standard rockcod) on short leaders. Salted pieces of *Engraulis mordax* and, to a lesser extent, *Scomber japonicus* were used as bait. Three to six tubs tied together formed a set. Usually, lines were set between the hours of 1000 and 1400 and retrieved the following day between 0600 and 1000.

Sinking and floating longlines were set. On sinking sets, weights (bricks) were tied to either end of the groundline and at intervals along the line. On floating sets, weights and floats (soda bottles) were tied alternately to groundline; the distance between two weights encompassed 50–60 hooks. Anchors and buoy lines were attached to each end of the groundline. Floating and sinking lines were set on mud, but only floating lines were set on banks. Sets on the mud ranged from 400 to 600 m deep; sets on the banks ranged from 350 to 550 m deep.

Scyliorhinid sharks were taken to the laboratory where they were measured to the nearest 1 mm total length (TL) and weighed to the nearest 0.1 g. The left clasper of males was measured to the nearest 0.5 mm. The gonads were removed and weighed to the nearest 0.1 g. All eggs larger than 4 mm in diameter were separated from the ovary and measured to the nearest 1 mm. Stomachs were removed and placed in 10% buffered formalin; the contents were

washed in water, sorted, and identified to the lowest taxon practicable; pieces of bait were ignored.

Size at sexual maturity was estimated for males by change in relative size of the claspers and testes, and for females by change in relative size of the ovaries and presence of egg cases in the oviducts (Pratt 1979). Polynomial regressions were fit to the data for males (SAS 1982). The reproductive season was determined by enlarged testes in the males and the presence of full-sized eggs in the ovaries of the females. The gonadosomatic index (GSI) was calculated for the sexes of both species from

$$\text{GSI} = (\text{gonad weight/body weight}) \times 100.$$

Analyses of stomach data were summarized by the index of relative importance (IRI) modified from Pinkas et al. (1971):

$$\text{IRI} = PO(PN + PW)$$

where PO is percent occurrence, PN is percent numbers, and PW is percent weight calculated for each prey category. The length of intact prey was measured.

Catch/effort data (where a unit of effort was one tub of line) were transformed to $\log_{10}$ and analyzed for habitat, season, and depth differences by analysis of covariance (ANCOVA) for unbalanced designs (SAS 1982) with habitat and season as the main effects and depth as the covariate. Catch per tub for each positive set was determined by averaging the catches of the constituent tubs.

Fish size data were analyzed for habitat, season, and depth differences by ANCOVA for unbalanced designs. The data were not transformed because size was approximately normally distributed.

Geometric mean weight-length regressions were calculated from the logarithmic transformation of

$$W = aL^b$$

where W is weight in grams, L is total length in millimeters, and a and b are fitted constants (Ricker 1973). The regression coefficients (b) were compared by the method of Clarke (1980).

The sediments of the upper continenal slope off Newport Beach are predominantly green silty clays. Sand content is fairly constant down slope (mean = 12% by dry weight); areas around the offshore banks and the shoulders of the submarine canyons are sandier (25–50% by dry weight). Organic content increases from 5 to 7% (as total volatile solids) at 290 m to 11–14% at 625 m (SCCWRP 1983[2]). Between 600 and 700 m, the slope gives way to the low-oxygen San Pedro Basin to the northwest and to the deeper San Diego Trough to the southeast (Fig. 1).

Longline fishermen recognize two habitats on the slope: hard substrate banks and soft, relatively featureless (on a fathometer) mud bottom. Surface sediments on the banks are a mixture of coarse sand, shell hash, and occasional rocks. As used herein, banks include submerged mountains, shoulders of submarine canyons, and isolated mounds as small as a few hundred meters across and 20–30 m high. The mud bottom is green silty clay and is the predominant habitat on the slope.

Oceanographic measurements in the water column off Newport Beach showed weak and decreasing gradients with increasing depth. The mean annual temperature was 8.3°C (SD = 0.3, N = 64, min = 7.5, max = 9.1) at 300 m and 6.5°C (SD = 0.2, N = 25, min = 6.0, max = 6.9) at 500 m. Mean annual dissolved oxygen was 1.21 ppm (SD = 0.26, N = 54, min = 0.76, max = 1.94) at 300 m and 0.48 ppm (SD = 0.10, N = 20, min = 0.31, max = 0.72) at 500 m. Some of the variation at 300 m was the result of seasonal changes related to upwelling. In the spring, temperature and dissolved oxygen decreased, and salinity and density increased (SCCWRP fn. 2).

RESULTS

Distribution and Abundance

The occurrence of scyliorhinid sharks in trawl catches was markedly different from longline catches. Catsharks were caught in 3 (6%) of the 48 otter trawls. The six individuals collected accounted for <0.1% of all fish caught in trawls. Catsharks were caught on 62 (87%) of the 71 longline sets (212 tubs of gear examined). The 698 individuals collected accounted for 5.8% of the fish caught (2.8% of catch weight) on longlines.

Apristurus brunneus were caught on 50 (70%) sets; 475 individuals were collected. *Parmaturus xaniurus* were caught on 53 (75%) sets; 223 individuals were collected. The two species occurred independently on the tubs of longline gear (χ^2 = 0.39, $P > 0.05$). They were equally abundant on bank

[2]SCCWRP. 1983. A survey of the slope off Orange County, California. Report to County Sanitation Districts of Orange County. Long Beach: Southern California Coastal Water Research Project, 208 p.

sets (t = 0.56, $P > 0.05$), but *A. brunneus* were more abundant than *P. xaniurus* on mud sets (t = 3.50, $P < 0.01$) (Table 1).

Apristurus brunneus occurred on 61% of the bank sets and 79% of the mud sets. Catches were not significantly different among habitats, seasons, or depths (ANCOVA, $P > 0.05$). Mean catch per tub in the mud habitat was not significantly different between floating and sinking sets (t = 1.35, P = 0.19).

Parmaturus xaniurus occurred on 73% of the bank sets and 76% of the mud sets. Catches were significantly higher on bank sets than on mud sets (ANCOVA, $P < 0.05$). Catches were nearly twice as high on bank sets in the winter compared with bank sets in the summer. Catch increased with increasing depth on banks, but it decreased with increasing depth on mud. Catches on the mud were not significantly different between floating and sinking sets (t = 0.76, P = 0.45.).

Size

There were no significant differences in the regression coefficients of the weight-length relationships between males and females of either *A. brunneus* or *P. xaniurus* over the range of sizes examined (Table 2; Fig. 2). There were no significant differences in the size of *A. brunneus* or *P. xaniurus* among habitats, seasons, or depths (ANCOVA, $P > 0.05$).

TABLE 1.—Catch statistics for *Apristurus brunneus* and *Parmaturus xaniurus* from longline collections on banks and mud. No. = number, wt = weight in kg, N = number of positive sets, $\bar{X}$ = mean, SD = one standard deviation.

		Banks			Mud		
Species		N	$\bar{X}$	SD	N	$\bar{X}$	SD
A. brunneus	No./tub	20	2.3	2.1	30	3.7	4.6
	Wt/tub	20	0.9	0.8	30	1.5	1.8
P. xaniurus	No./tub	24	2.0	2.0	29	1.1	1.1
	Wt/tub	24	0.6	0.6	29	0.4	0.4

Reproduction

Based on relative change in clasper length and gonad weight, *A. brunneus* males reached sexual maturity between 450 and 500 mm TL; *P. xaniurus* males reached sexual maturity between 375 and 425 mm TL (Fig. 3). Females of both species reached sexual maturity between 425 and 475 mm TL (Fig. 4). Only the right ovary was functional in both species.

Seasonal changes in gonadal development were not pronounced among *A. brunneus*. Male and female GSIs were highest in winter and lowest in summer (Fig. 5). Large oocytes were present in the right ovary of females throughout the year (Fig. 6).

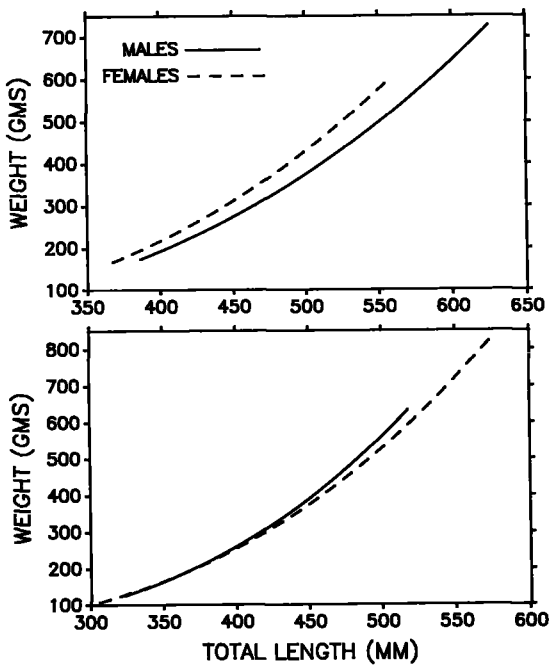

FIGURE 2.—Weight-length relationships of *Apristurus brunneus* (above) and *Parmaturus xaniurus* (below).

TABLE 2.—Geometric mean weight-length regressions for *Apristurus brunneus* and *Parmaturus xaniurus*. N = sample size, min = minimum total length (TL) in mm, max = maximum TL, W = body weight in g, L = TL, $L1$ = lower 95% confidence interval for b, $L2$ = upper 95% confidence interval, r = correlation coefficient.

Species	Sex	N	min	max	$W = aL^b$	$L1$	$L2$	r
A. brunneus	F	149	369	556	$W = 2.379 \times 10^{-6} L^{3.059}$	2.839	3.279	0.899
	M	90	389	625	$W = 3.577 \times 10^{-6} L^{2.971}$	2.809	3.134	0.966
P. xaniurus	F	76	307	574	$W = 9.377 \times 10^{-7} L^{3.242}$	3.045	3.439	0.965
	M	89	325	516	$W = 3.163 \times 10^{-7} L^{3.427}$	3.166	3.688	0.934

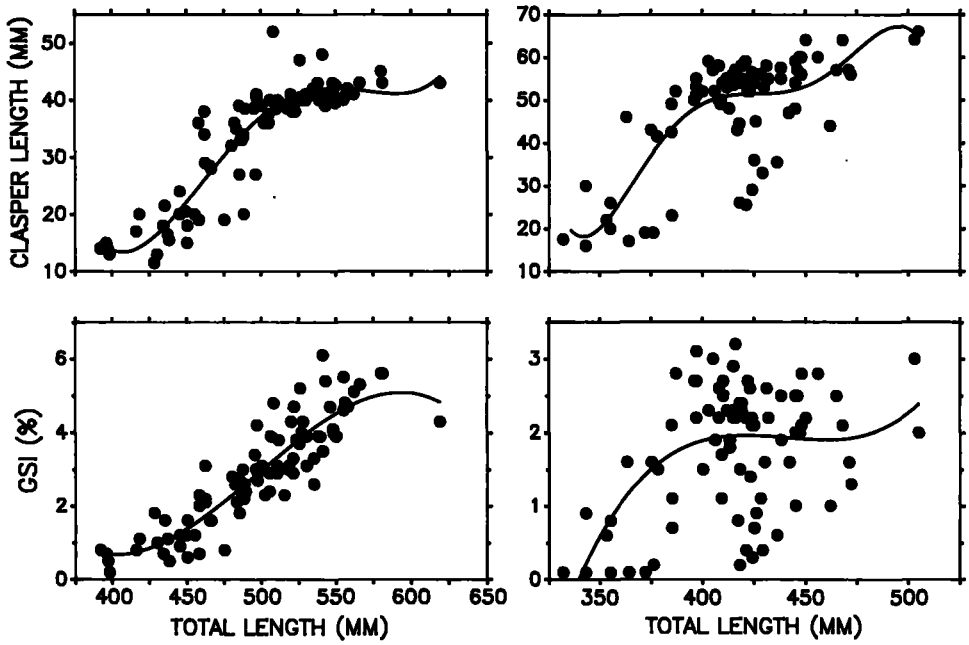

FIGURE 3.—Left clasper length and gonadosomatic index (GSI) versus total length of male *Apristurus brunneus* (left) and *Parmaturus xaniurus* (right).

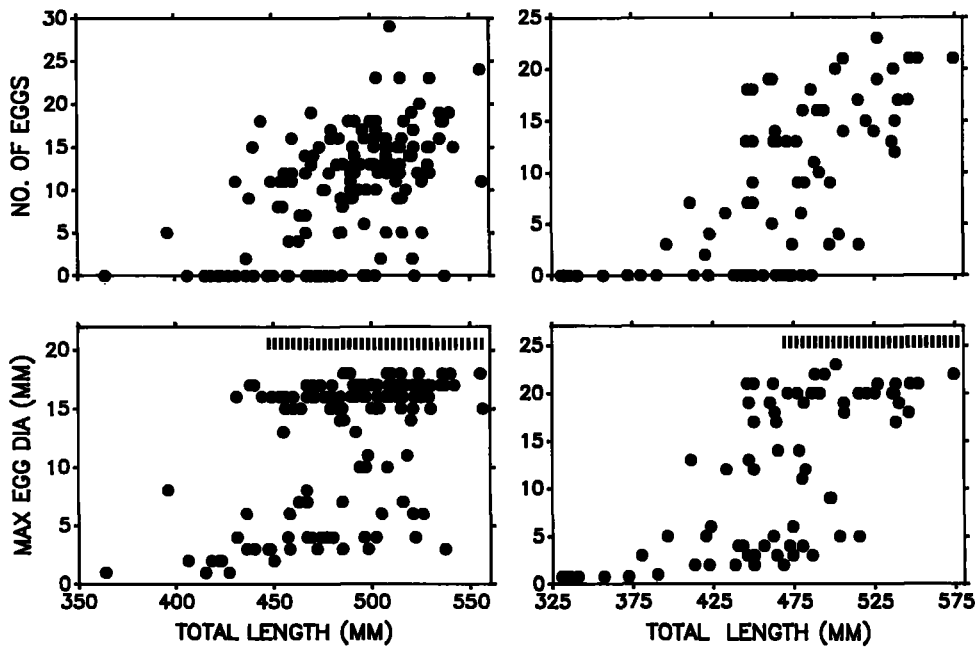

FIGURE 4.—Number of oocytes (>4 mm) and maximum oocyte diameter versus total length of female *Apristurus brunneus* (left) and *Parmaturus xaniurus* (right). Cross-hatched bar indicates size of fish carrying egg cases.

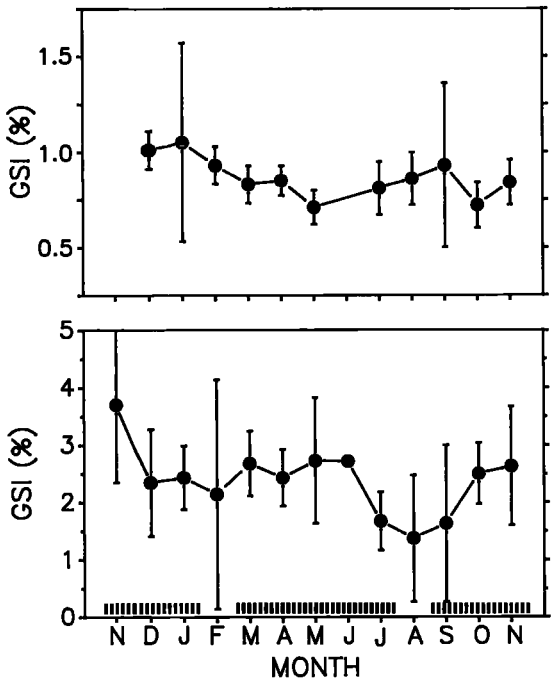

FIGURE 5.—Mean gonadosomatic index (GSI) of *Apristurus brunneus* males (above) and females (below) from November 1983 through November 1984. Cross-hatched bar indicates months when females were carrying egg cases. Vertical bars are 95% confidence intervals.

The number of oocytes larger than 4 mm was correlated with size among mature females (r = 0.425, $P < 0.001$); the maximum number was 29. Atretic oocytes were observed from March through November and spent fish (no oocytes larger than 2–3 mm; N = 2) were collected in December and July.

Egg cases were found in the oviducts of 48 *A. brunneus* females larger than 450 mm (37% of mature females); the egg cases were not completely formed in only one individual. Females with egg cases were collected every month except February and August (Fig. 5). More mature females carried egg cases from December through May (42%) than from June through November (29%), although the difference was not significant (χ^2 = 2.24, $P > 0.1$). Egg case length (measured between the tendrils) was correlated with female total length (r = 0.386, $P < 0.02$). The mean ratio of egg case length to female total length was 0.114 (SD = 0.019).

Seasonal changes in gonadal development were not pronounced among *P. xaniurus*. Male GSI was high throughout the year; female GSI was highest in winter and lowest in summer (Fig. 7). Large

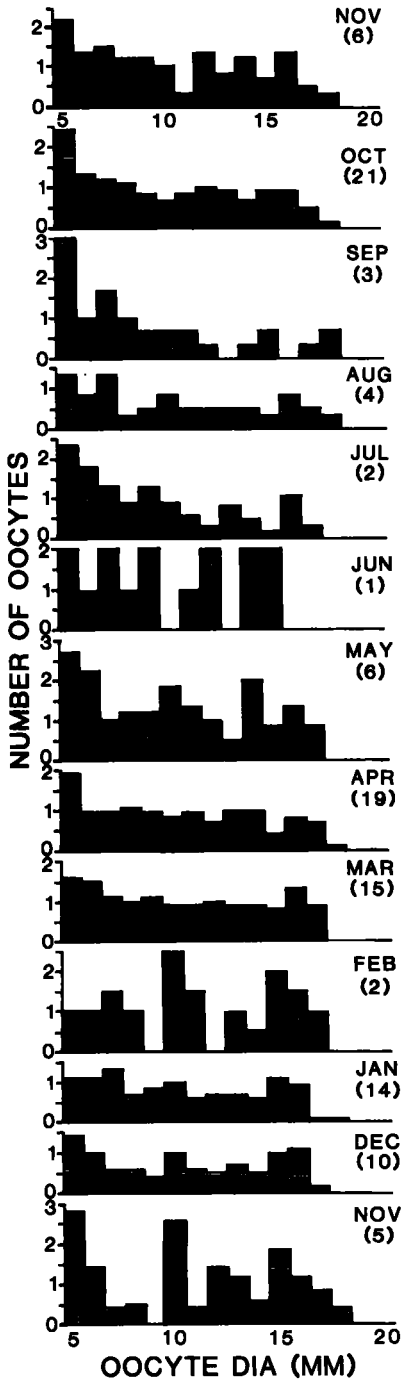

FIGURE 6.—Mean monthly oocyte (>4 mm) size-frequency distribution of *Apristurus brunneus* from November 1983 (bottom) to November 1984 (top). Sample size in parentheses.

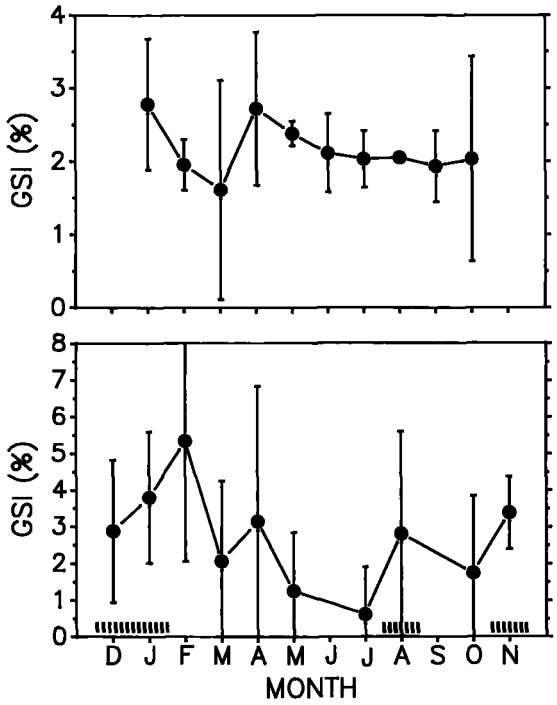

FIGURE 7.—Mean gonadosomatic index (GSI) of *Parmaturus xaniurus* males (above) and females (below) from December 1983 through November 1984. Cross-hatched bar indicates months when females were carrying egg cases. Vertical bars are 95% confidence intervals.

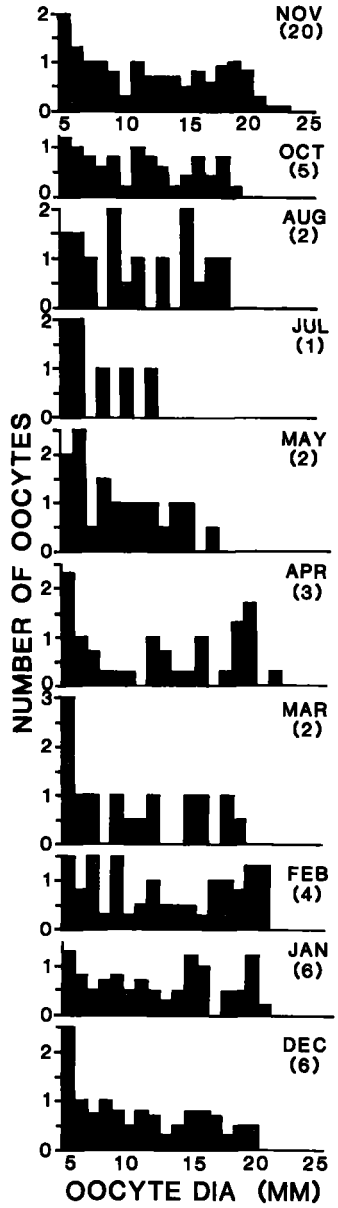

FIGURE 8.—Mean monthly oocyte (>4 mm) size-frequency distribution of *Parmaturus xaniurus* from December 1983 (bottom) to November 1984 (top). Sample size in parentheses.

oocytes were present in the right ovary of females every month except July (Fig. 8). The number of oocytes larger than 4 mm was correlated with size among mature females ($r = 0.597$, $P < 0.001$); the maximum number was 23. Atretic oocytes were observed in May, August, and November and spent fish (no oocytes larger than 3–4 mm; $N = 3$) were collected in January and March.

Egg cases were present in the oviducts of five *P. xaniurus* females larger than 470 mm (10% of mature females); the egg cases were not completely formed in one individual. One 450 mm TL female had recently released two egg cases as evidenced by distended oviducts. Egg cases were present in females collected in December, January, August, and November (Fig. 7). The mean ratio of egg case length to female total length was 0.156 (SD = 0.023).

Food Habits

Stomachs from 211 *A. brunneus* were examined; 138 (65%) were empty or contained only traces of well-digested prey. There was no seasonal trend in the proportion of empty stomachs. Crustaceans, teleosts, and molluscs constituted the diets of the remaining individuals (Table 3). Natantian decapods

TABLE 3.—Stomach contents of 73 *Apristurus brunneus* (mean size = 496 mm TL, SD = 40, min = 396, max = 619). *PO* = percent occurrence, *PN* = percent number, *PW* = percent weight, IRI = index of relative importance.

	PO	*PN*	*PW*	IRI
Crustacea	97.3	74.2	67.3	13,768
Isopoda	9.6	3.0	0.8	36
Epicaridea	9.6	3.0	0.8	36
Mysidacea	1.4	0.5	0.4	1
Euphausiacea	6.8	4.5	4.5	61
Decapoda	71.2	61.8	58.4	8,558
Natantia	61.6	52.7	48.9	6,259
Penaeidea	13.7	7.5	6.6	193
Sergestidae	12.3	5.6	4.7	127
Sergestes similis	11.0	4.9	3.9	97
Petalidium suspiriosum	1.4	0.7	0.8	2
Penaeidae	2.7	1.9	1.8	10
Bentheogennema sp.	2.7	1.9	1.8	10
Caridea	45.2	23.7	28.8	2,373
Pasiphaeidae	45.2	23.7	28.8	2,373
Pasiphaea sp.	27.4	14.0	16.3	830
Pasiphaea pacifica	13.7	5.1	8.3	184
Pasiphaea emarginata	1.4	1.4	1.4	4
Reptantia	15.1	6.6	7.8	217
Anomura	15.1	6.6	7.8	217
Galatheidae	15.1	6.6	7.8	217
Pleuroncodes planipes	5.5	1.9	2.0	21
Mollusca	20.5	8.4	11.4	406
Pelecypoda	1.4	0.3	0.1	<1
Cephalopoda	19.2	8.0	11.2	369
Coleoidea	19.2	8.0	11.2	369
Decapoda	19.2	8.0	11.2	369
Teuthoidea	19.2	8.0	11.2	369
Gonatus sp.	4.1	2.5	3.3	24
Abraliopsis felis	2.7	0.8	1.0	5
Loligo opalescens	1.4	0.5	0.8	2
Osteichthyes	42.5	16.6	21.0	1,598
Myctophidae	6.8	3.8	4.4	56

(40% of total IRI), especially carideans of the family Pasiphaeidae (15%), dominated the contents. Teleosts (10%), including myctophids, were also important. Most fish remains in the stomachs were digested beyond recognition. Squids made up the remainder of the diets (3%). There was no evidence for a size-related change in diet; the dominant prey occurred in all sizes of fish examined.

The stomachs of 73 *A. brunneus* contained an average of 2.7 prey items (SD = 1.7, max = 10) and the contents averaged 0.7% of body weight (SD = 0.4, max = 1.99). Content weight was not correlated with body weight (Spearman $r_s = 0.227$, $P > 0.2$), and carapace length of the most frequently occurring prey, *Pasiphaea* spp., was not correlated with fish size ($r_s = -0.168$, $N = 33$, $P > 0.2$). Relative content weight was not significantly different among months (Kruskal-Wallis test, $H = 14.89$, $P = 0.19$).

Stomachs from 155 *P. xaniurus* were examined; 85 (55%) were empty or contained only traces of well-digested prey. There was no seasonal trend in the proportion of empty stomachs. Crustaceans, teleosts, and molluscs constituted the diets of the remaining individuals (Table 4). Reptantian decapods (36% of total IRI), particularly the galatheid *Pleuroncodes planipes* (12%), dominated the contents. Natantian decapods (3%) and teleosts (7%), including myctophids, were also important. Most fish remains in the stomach were digested beyond recognition. Squids made up a small part of the diets (<1%). There was no evidence for a size-related change in diet; the dominant prey occurred in all sizes of fish examined.

The stomachs of 70 *Parmaturus xaniurus* contained an average of 2.4 prey items (SD = 1.3, max = 5) and the contents averaged 1.2% of body weight (SD = 0.9, max = 4.7). Content weight was correlated with body weight (Spearman $r_s = 0.372$, $P < 0.002$). Relative content weight was not significantly different among months (Kruskal-Wallis test, $H = 13.26$, $P = 0.35$).

TABLE 4.—Stomach contents of 70 *Parmaturus xaniurus* (mean size = 438 mm TL, SD = 47, min = 341, max = 547). *PO* = percent occurrence, *PN* = percent number, *PW* = percent weight, IRI = index of relative importance.

	PO	*PN*	*PW*	IRI
Crustacea	97.1	75.5	72.1	14,332
Isopoda	4.3	1.6	0.5	9
Epicaridea	4.3	1.6	0.5	9
Bopyridae	2.9	1.0	0.3	4
Munidon parvum	2.9	1.0	0.3	4
Euphausiacea	24.3	8.6	5.4	340
Decapoda	81.4	56.5	59.2	9,421
Natantia	21.4	10.8	11.9	486
Penaeidea	11.4	4.6	4.0	98
Sergestidae	11.4	4.6	4.0	98
Sergestes similis	11.4	4.6	4.0	98
Caridea	12.9	5.0	7.0	155
Pasiphaeidae	12.9	5.0	7.0	155
Pasiphaea pacifica	10.0	4.0	5.8	98
Reptantia	67.1	38.5	43.4	5,495
Anomura	65.7	38.2	43.0	5,335
Galatheidae	65.7	38.2	43.0	5,335
Pleuroncodes planipes	40.0	21.9	26.1	1,920
Brachyura	1.4	0.4	0.4	1
Mollusca	5.7	1.4	1.8	18
Cephalopoda	5.7	1.4	1.8	18
Coleoidea	5.7	1.4	1.8	18
Decapoda	5.7	1.4	1.8	18
Teuthoidea	5.7	1.4	1.8	18
Osteichthyes	48.6	20.8	25.3	1,036
Myctophidae	10.0	4.8	6.1	109

DISCUSSION

Distribution and Abundance

Apristurus brunneus and *Parmaturus xaniurus* were a common, though unwanted, part of the longline catch on the upper continental slope off southern California. The abundance of both species was underestimated by trawl. Among the 29 species (12,074 individuals) caught on longlines, *A. brunneus* ranked 7th in abundance and *P. xaniurus* ranked 10th. They ranked 29th and 34th, respectively, among the 42 species (7,264 individuals) taken in trawls (Cross 1987). The bias of small trawls against large demersal fishes is well known (Day and Pearcy 1968; Haedrich et al. 1975). Most previous fish collections on the slope off southern California were taken with small trawls which explains why these sharks are not considered common.

Catches of *A. brunneus* and *P. xaniurus* were similar on bank sets, but *A. brunneus* was more abundant on mud sets. The two species occurred independently at the scale of one tub of longline gear (about 650 m). *Apristurus brunneus* was equally abundant on mud and bank sets, and seasonal differences in distribution and catch were not apparent. *Parmaturus xaniurus* was more abundant on bank sets than on mud sets, suggesting some habitat selection. Catches of *P. xaniurus* were highest on banks in the winter; the reason for this is not known.

Juvenile *A. brunneus* and *P. xaniurus* were conspicuously absent from longline and trawl collections on the slope. Catsharks are generally regarded as demersal fishes (Compagno 1984), but *A. brunneus* and *P. xaniurus* have been captured in the water column. An undisclosed number of *A. brunneus* larger than 260 mm (TL assumed) were collected up to 172 m above the bottom in 373 m of water off British Columbia, Canada (Jones and Geen 1977). Sixty-nine *P. xaniurus* (99–320 mm) were collected in 43 midwater trawls from 9 to 490 m above the bottom in 527–582 m of water in the Santa Barbara Basin, CA (Lee 1969). The livers of *P. xaniurus* contain a high proportion of squalene, a low specific gravity oil that aids in hydrostatic balance (Springer 1979).

Juveniles and adolescents of both species were taken in midwater trawls in the Santa Barbara Basin (bottom depths between 490 and 576 m) (UCSB[3]). Catsharks occurred in 31 (41%) of 75 mid-

[3]UCSB. Collections taken by the University of California, Santa Barbara, with an opening and closing net between 1965 and 1967 and deposited in the Los Angeles County Museum of Natural History.

water trawls; 83% of the individuals were collected within 250 m of the bottom. Fifty-four *A. brunneus* (99–380 mm TL, median = 177) were collected in 22 trawls and 23 *P. xaniurus* (110–229 mm TL, median = 175) were collected in 17 trawls.

The occurrence of juveniles and adolescents of both species in midwater collections suggests that the water column, especially within 200–300 m of the bottom, is their nursery area, and would explain their conspicuous absence in benthic collections during the present study. Cailliet[4] also concluded that *P. xaniurus* are mesopelagic as juveniles and demersal as adults.

Interestingly, 119 midwater trawls in the Santa Cruz Basin, CA and near Rodriguez Seamount (most bottom depths between 1,200 and 2,200 m) (UCSB fn 3) captured no scyliorhinid sharks (the trawls were taken concomitantly with trawls in the nearby Santa Barbara Basin). Bottom depths >1,000 m may be beyond the range of both species. The deepest recorded collection of *A. brunneus* off southern California was 933 m (Roedel 1951); the deepest recorded collection of *P. xaniurus* was 687 m (Springer 1979). The absence of both species in midwater trawls in the Santa Cruz Basin and near Rodriguez Seamount would not be surprising if juveniles do not travel far horizontally and adults do not occur below 1,000 m.

Size

The largest *A. brunneus* collected during the present study (625 mm TL male) was less than the maximum recorded size (680 mm TL; Compagno 1984). The largest *P. xaniurus* (574 mm TL female) was greater than the maximum recorded size (550 mm TL; Compagno 1984). Weight-length relationships of males and females of both species were similar. It is not known if males and females that were the same size were the same age. Attempts at determining the ages of *P. xaniurus* were unsuccessful (Cailliet 1986[5]).

Reproduction

Like many scyliorhinid sharks, *A. brunneus* and *P. xaniurus* exhibit single oviparity: one fertilized egg enters each oviduct and, after a short period, is deposited in a tough egg case on the substrate where it is anchored by tendrils (Nakaya 1975). Embryonic development takes place largely outside the mother and may require a year to produce a hatchling (Compagno 1984).

Size at sexual maturity estimated during the present study agrees with published observations for both species (Jones and Geen 1977; Compagno 1984). Male *P. xaniurus* matured at a smaller size than male *A. brunneus*. Females of both species matured at about the same size and fecundity increased with female size. Fecundity was greater among *A. brunneus* as was the proportion of mature females carrying egg cases, but the proportion of body weight devoted to gonads and maximum oocyte size were greater among *P. xaniurus*.

Seasonal changes in gonadal development were not well defined for either species; individuals in both populations may be sexually active at any time of the year. Several observations suggest that oocyte production was seasonal: the highest proportion of adult females with oocytes <10 mm in diameter and the highest frequency of atretic oocytes were observed from summer through fall when GSI was lowest.

There are few published observations on reproductive cycles of scyliorhinid sharks. *Scyliorhinus canicula*, an abundant shelf and upper slope catshark in the northeastern Atlantic Ocean, lays eggs throughout the year. Seasonal maxima in egg capsule production are apparent, but timing varies with latitude. Size at sexual maturity also varies with latitude; fish mature at a larger size at higher latitudes (Ford 1921; Capapé 1977). The fecundity of female *S. canicula* (46–50 cm TL) ranges from 23 to 34 eggs; fecundity increases with fish size. Eggs are 16 mm in diameter at ovulation. Annual fecundity is about 96–115 eggs. In the Mediterranean Sea, egg capsule incubation times range from 180 days for eggs deposited during the summer to 285 days for eggs deposited during the winter (Capapé 1977).

Food Habits

Apristurus brunneus and *Parmaturus xaniurus* consumed, in order of importance, crustaceans, teleosts, and squids. Similar diets were reported for both species by Jones and Geen (1977), Cailliet (1981, see fn. 4), and Compagno (1984). The diets of the two catsharks were broadly similar except for the occurrence of crustaceans. Reptantian decapods

[4]Cailliet, G. M. 1981. Ontogenetic changes in the depth distribution and feeding habits of two deep-dwelling demersal fishes off California: sablefish and filetail cat sharks. [Abstr.] Am. Soc. Ichthyol. Herpetol. Sixty-first Annu. Meeting, Corvallis, OR.

[5]G. M. Cailliet, Moss Landing Marine Laboratories, Moss Landing, CA, pers. commun. July 1986.

dominated the diet of *A. brunneus* (36% of total IRI) while natantian decapods dominated the diet of *P. xaniurus* (40% of total IRI). This may be a result of habitat differences between the catsharks rather than prey selection. The epicaridean isopods in the stomach contents are crustacean parasites, and were probably ingested with their hosts.

A very high percentage of *A. brunneus* and *P. xaniurus* stomachs was empty. This may not be representative of their respective populations. Sharks caught by baited hooks have a higher proportion of empty stomachs, and lower stomach content weight, than sharks caught by gill net (Medved et al. 1985).

Most of the prey consumed by *A. brunneus* and *P. xaniurus* are pelagic. Demersal adult *P. xaniurus* eat mostly crustaceans (including pelagic pasiphaeid and sergestid shrimps), fishes (primarily myctophids), and cephalopods. Mesopelagic juveniles eat more and smaller pelagic pasiphaeid, euphausiid, and sergestid shrimps and cephalopods, and fewer fishes (Cailliet fn. 4). Similar pelagic prey also dominate the diets of *Galeus melastomus* and *Apristurus* spp., common outer shelf-upper slope scyliorhinid sharks of the northeastern Atlantic Ocean (Orsi and Wurtz 1977; Mattson 1981; Mauchline and Gordon 1983). Ontogenetic changes in diet were reported for *Scyliorhinus canicula*: the importance of crustaceans declines and the importance of teleosts increases with increasing fish size (Capapé 1974).

Deep-sea benthic fishes can obtain pelagic prey by 1) feeding on prey whose vertical distribution extends close to the bottom [*P. xaniurus* were observed eating moribund myctophids in the bottom of the Santa Barbara Basin (Springer 1979)]; 2) migrating into the water column to feed [*A. brunneus* and *P. xaniurus* are captured in midwater (Jones and Geen 1967; Lee 1969; UCSB fn. 3)]; 3) feeding on carcasses that sink to the bottom (mud and terrestrial plant debris were found in several catshark stomachs during the present study, and both species took dead bait); or 4) feeding in the net (not a factor in this study) (Pearcy and Ambler 1974; Pearcy 1976; Sedberry and Musick 1978).

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FURTHER SUPPORT FOR THE HYPOTHESIS THAT INTERNAL WAVES CAN CAUSE SHOREWARD TRANSPORT OF LARVAL INVERTEBRATES AND FISH

ALAN L. SHANKS[1]

ABSTRACT

In areas of mesotides (tidal range 2 to 4 m) and narrow continental shelves (<30 km) internal waves can transport (i.e., convey from one place to another) the larvae of coastal organisms shoreward. Research reported here was in an area of microtides (tidal range <2 m) and a wide continental shelf (>80 km), the South Atlantic Bight. Half of the sampled sets of internal waves were aligned parallel to shore and probably originated at the shelf break. The higher densities of larvae and flotsam in the slicks over these internal waves (convergence zones) than in the rippled water between slicks (divergence zones) indicates that these waves were transporting larvae and flotsam shoreward. All nontransporting internal waves were aligned at a sharp angle to shore and may have formed over shoals oriented perpendicular to shore.

To further test the hypothesis that internal waves can transport larvae, surface plankton were collected from the waters over, in front, and behind a set of internal waves. The density of *Portunus* spp. megalopae was significantly higher in waters in front of the set than behind. The average densities of a variety of larval fish and invertebrates were significantly higher over the internal waves than in front of the set of waves. These data indicate that internal waves can cause shoreward transport of larvae and flotsam. Precompetent larval fish were not carried shoreward by this set of waves while competent stages (i.e., juvenile through postflexion) were transported shoreward.

Recent papers have suggested that the planktonic larvae of some coastal invertebrates and fish (Shanks 1983, 1985, 1986; Jillett and Zeldis 1985; Kingsford and Choat 1986; Shanks and Wright 1987) as well as flotsam (e.g., an oil spill, Shanks 1987) can be transported (i.e., conveyed from one place to another) by internal waves. As the tide ebbs off the continental shelf or across some other sharp change in the bottom relief (i.e., a reef or bank) a lee wave is formed (Lee and Beardsley 1974; Gargett 1976; Maxworthy 1979). When the tide changes to flood this lee wave is "released" and propagates away from its point of origin (see for example Chereskin 1983). Most of the waves formed at the continental shelf break propagate shoreward. As the original internal wave moves onshore it evolves from a solitary wave into a set of waves (Osborne and Burch 1980). Stripes of glassy water, slicks, are surface manifestations of currents over the internal waves, and they delineate zones of converging and downwelling currents situated between the crest and the trough of an internal wave (Ewing 1950; LaFond 1959). The currents over the internal waves generate slicks by both perturbing small surface waves and concentrating the organic surface film (Ewing 1950; Gargett 1976). Buoyant flotsam will be carried into the convergence zone by the surface currents, but because of the particle's buoyancy they will not follow the water as it is downwelled; the flotsam will be trapped at the surface in the convergence and as the convergence zone moves onshore so will the flotsam. The proposed mechanism of larval transport suggests that any organism which can remain at the surface in the convergence zone either by swimming or other behaviors (Shanks 1985) will, like flotsam, remain in the slick and be transported onshore (Shanks 1983).

The conditions necessary for the production of tidally generated internal waves (tides, sharp bottom relief, and some water column density stratification) are present in the waters adjacent to nearly all land masses, and the surface manifestations of internal waves have been observed from both ships and satellites in numerous locations (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Evidence that internal waves may be capable of transporting planktonic larvae onshore has been collected in the Pacific Ocean off Southern California (Shanks 1983, 1985, 1986), in the San Juan Archipelago (Shanks and Wright 1987), and in the waters off the North

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and South Islands of New Zealand (Zeldis and Jillett 1982; Jillett and Zeldis 1985; Kingsford and Choat 1986). These areas are characterized by mesotides, i.e., tidal range 2 to 4 m (Davis 1964). The first purpose of the research reported in this paper was to test if transport occurred in the Atlantic Ocean and in an area of microtides (tidal range <2 m, Davis 1964), the South Atlantic Bight.

To date researchers have compared the density (no./m^2) of larvae in the convergence zones (slicks) over internal waves to the density present in the divergence zone (ripples). Cases where the densities of larvae were significantly higher in slicks than the ripples were used as evidence for the proposed hypothesis. Higher density in the convergence implies that larvae tend to spend more time in the slick than in the water between slicks. Because of the speed at which internal waves are propagating, even a brief residence in an internal-wave-slick could cause appreciable shoreward transport. For example, if a larvae spent an hour in a slick it could be carried about 2 km (assuming an average internal wave speed of 56 cm/s, Sawyer 1983).

Higher larval densities in the convergence zone is only one of several predictions which should be true if internal waves are transporting larvae shoreward. The second purpose of this research was to test several additional predictions. As an internal wave moves shoreward, larvae from in front of the wave will be swept by the currents associated with the wave into the convergence zone. If these larvae can remain at the surface in the convergence, they will be carried shoreward. Predictions include 1) larval density in the waters in front of the set of internal waves should be significantly higher than in the waters behind the set; 2) because larvae will accumulate in the convergence, the observed density of larvae over an internal wave will be significantly higher than the density in the waters in front of the set of internal waves; and 3) a rare larval type may be carried into an area from a distant source in which case these particular larvae may only be present in the waters over the internal wave and will be concentrated in the slicks. To test these predictions, replicate neuston net samples were collected in the convergence and divergence zones over a set of internal waves, and in the waters immediately in front and behind this set of internal waves.

METHODS

The study was confined to the ocean waters at the northern end of Onslow Bay within about 20 km of Beaufort Inlet, NC, U.S.A. (long. 34°40′W, lat. 76°40′N; Fig. 1). Surface plankton tows from the waters over internal waves were collected during the summer of 1985 on 4 and 24 June, 14 and 20 July, and 21 August. On 24 June 1985 surface plankton tows were also collected from immediately in front and behind a set of internal waves. On 14 June 1985 and 9 and 19 June 1986 samples were collected at the surface and in the water column to determine which taxa were exclusively neustonic in distribution.

Winds stronger than 10 to 15 knots obliterate the slicks, which delineate the convergence zones over internal waves. Searches for internal-wave-slicks and sampling of the associated plankton were limited to periods with winds less than a moderate breeze (Beaufort scale 4). The procedure for locating internal-wave-slicks was to proceed along shore until the estuarine front associated with Beaufort Inlet was crossed and thence perpendicular to shore until we found a set consisting of at least three large (at least 30 m wide by about 500 m long) linear slicks separated by one to several hundred meters of rippled water. Sets of large slicks separated by rippled water are a unique surface signature of large, usually tidally generated internal waves (Ewing 1950; LaFond 1959; Apel et al. 1975; Gargett 1976; Fu and Holt 1982; Chereskin 1983; Sawyer 1983).

To test if a set of internal waves was capable of transporting flotsam, surface drifters (weighted Styrofoam cups) were released in a line perpendicular to and in front of the set of internal-wave-slicks (Shanks 1983). Prior to the release of the surface drifters and immediately after all sampling was completed the position of the first slick in the set was determined by either compass bearings on landmarks or with loran. From these measurements we were able to determine the distance that the set of waves propagated during the period of observation.

While the currents acted on these surface drifters, 3 or 4 replicate 5- to 10-min surface (<20 cm depth) plankton tows were made in the slicks and rippled water between slicks. These 1985 samples were collected on 4 and 24 June, 14 and 20 July, and 21 August 1985. In addition, on 24 June 1985 replicate surface plankton samples were also collected from the water immediately in front and behind the set of internal waves (within 200 m of the internal wave set). Plankton samples were collected using a manta net (Brown and Cheng 1981) with a mouth opening of 0.95 × 0.26 m and a net mesh of 0.333 mm. A flow meter mounted in the mouth of the net measured the volume of water filtered. Between tows

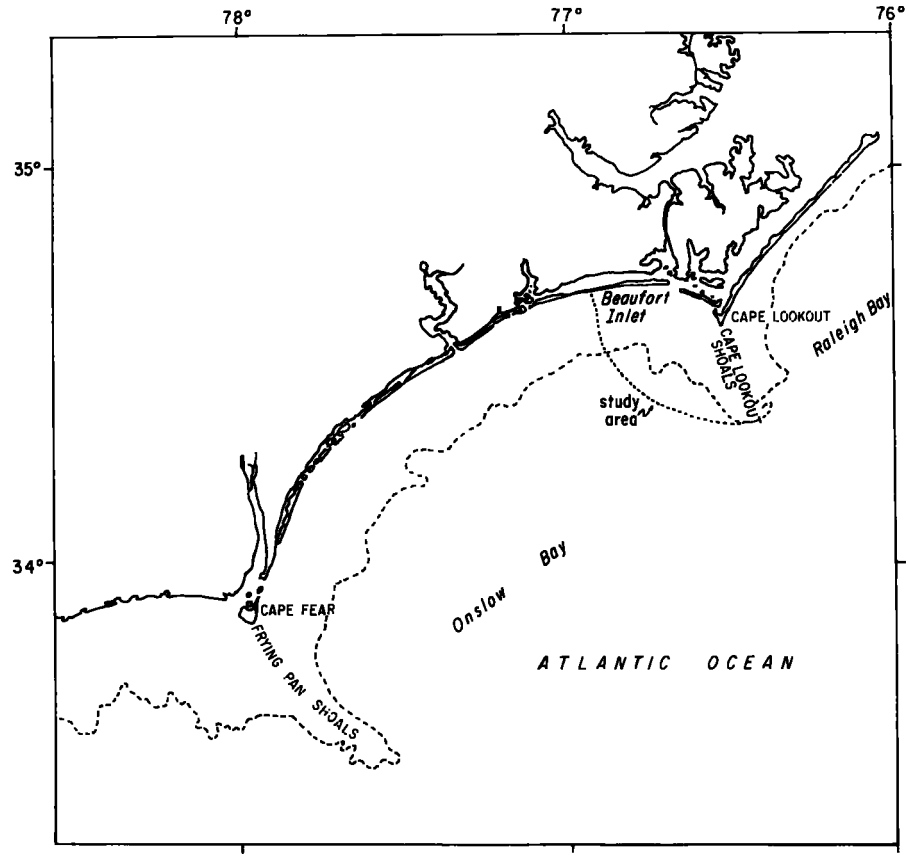

FIGURE 1.—Map of the study area. The dashed line running along shore is the 20 m contour and the dashed line running from just to the left of Beaufort Inlet to the tip of Cape Lookout Shoals encloses the study area.

in the different habitats the manta net was cleaned by towing for 5 to 10 minutes with the cod end removed. Most of the plankton was washed from the net by this procedure. For convenience and in order to more accurately sample the relatively small environments studied these plankton tows were made from a 6 m motor boat. Plankton samples were preserved in 5% formalin.

To assess the vertical distribution of larval types, surface and oblique plankton tows were made on 14 June 1985 and 9 June 1986. On 19 June 1986 replicate (n = 3) surface, oblique, and bottom tows were made. The dimensions of the oblique and bottom sled nets were 0.55 × 0.55 m and 0.80 × 0.45 m respectively. Both nets had mesh of 0.333 mm, and flow meters on the nets were used to measure the volume of water filtered. The procedure for the oblique tows was as follows: with the boat moving slowly forward the net was lowered rapidly to near the bottom (about 10 to 20 m) and then, maintaining a wire angle of about 60°, the net was hauled slowly to the surface. The bottom tows were made by lowering the sled straight to the bottom with the boat stationary; as the boat moved slowly forward, the line was paid out until a scope of 1 to 3 was achieved; tows lasted 5 to 10 minutes; at the end of the tow the boat was backed down onto the net; and the net was pulled vertically back to the surface. Both the oblique and bottom nets were open when they passed through the surface and were thus contaminated by some surface plankton.

Organisms were sorted and identified with the aid of a dissecting microscope. A variety of sources were used to identify larval fish (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978; Fahay 1983). Larval fish were also sorted by developmental stage which were defined following the terminology and descriptions in Ahlstrom et al.

(1976) and Moser and Ahlstrom (1970). Megalopae were identified from references sited in Williams (1984). *Portunus* spp. and *Callinectes* spp. megalopae were separated using the characters suggested by Smyth (1980). Penaeids were identified using Cook (1966). No attempt was made to precisely identify the other groups of organisms counted.

Statistical comparisons of the density of larvae and flotsam in the different sampled habitats were made using Wilcoxon's two-sample test (Sokal and Rohlf 1969). Densities were considered to be significantly different when $P \leq 0.05$.

RESULTS

During the summer of 1985 searches for internal-wave-slicks were made on eight occasions. On three days, despite favorable wind and sea conditions, no internal-wave-slicks were observed. On 4 and 24 June, the observed sets of slicks were oriented parallel to shore and the bottom topography while on 14 and 20 July sets were oriented nearly perpendicular to shore. On 21 August a set of slicks aligned nearly perpendicular to shore was observed about 5 km offshore, and at about 9 km offshore a second set of slicks was found oriented parallel to the bottom topography. Both types of slicks, perpendicular and parallel orientation, possessed all of the usual characteristics of internal waves. Slicks were about 30 to 50 m wide, they were separated by one to several hundred meters of rippled water, and the sets moved (the parallel-to-shore slicks moved onshore while the perpendicular-to-shore slicks moved north).

The surface drifters released in front of sets of slicks oriented parallel to shore on 4 June and 21 August could not be located following the plankton tows. On 24 June, all of the drifters located at the end of the plankton tows (48 of 50 released) were found in the first two slicks of the set of internal waves. The drifters, which had been released in a 250 m long line in front of the set of internal waves, had been caught, concentrated, and carried about 4 km shoreward by the internal waves. Clearly this set of internal waves was capable of carrying buoyant flotsam shoreward.

Sargassum floats were abundant in the plankton tows. The floats are buoyant, do not extend above the water (i.e., are not blown directly by the wind), and, hence, the floats should act much like the released surface drifters. On all three dates when the internal-wave-slicks were oriented parallel to shore, the density of Sargassum floats was significantly higher (14- to 300-fold higher; Tables 1, 2) in the convergence than divergence zones. These data indicate that not only was the set of internal waves sampled on 24 June capable of carrying flotsam shoreward, but the sets oriented parallel to shore on 4 June and 21 August were also capable of carrying buoyant flotsam shoreward.

In contrast, on those days when the slicks were oriented roughly perpendicular to shore (14 July, 20 July, and 21 August, Table 1) released surface drifters were about equally distributed between slick and rippled water and, despite the fact that the slicks moved northward during the observation period, the drifters were not carried along with the waves. The density of Sargassum floats was not significantly higher in the slicks than the rippled water between the slicks. These data suggest that these internal waves were not transporting flotsam.

Before larval densities can be interpreted, it is first necessary to determine which larval types are found exclusively in the neuston. An increase in the neustonic density of organisms, which inhabit both the neuston and the water column, could be due to forces concentrating just the neustonic portion of the population, or it could be due to animals from the water column augmenting the population in the neuston. Given the sampling regime of this study it was impossible to differentiate between these two possibilities. Because of this limitation a series of tows were made in the neuston, the water column, and bottom water to determine which organisms exclusively inhabited the neuston.

There was a distinct assemblage of megalopae and larval fish that were caught in the oblique water column and bottom plankton tows but were nearly absent from the neuston tows (Table 3). Unfortunately, organisms that were common in the neuston tows made over or around internal waves were abundant on only one of the three dates when the vertical distribution samples were collected. On this one date (19 June 1986, Table 3) there was a group of larval fish and crabs that were only present in the neuston tows. This latter group included the megalopae of *Portunus* spp. and *Callinectes* spp., juvenile *Monacanthus hispidus*, and juvenile and larval *Hyporhamphus unifasciatus* and *Sphoeroides maculatus*. Previous research also suggests that these larvae and postlarvae as well as others are inhabitants of the surface waters. Both the behavior (Sulkin andVan Heukelem 1981) and the vertical distribution (Smyth 1980; Johnson 1985a) of *Callinectes* spp. megalopae suggest that they are usually neustonic. The megalopae of *Portunus* spp. and

TABLE 1—The density of larval fish and invertebrates (mean no./100 m^2 ± SE) in the slicks (convergence zones) and ripples (divergence zones) over internal waves and the relative concentration of these organisms in the slicks (i.e., the ratio of slicks/ripples) over internal waves oriented parallel (data in upper section of table) and perpendicular (data in lower section of table) to shore.

	Dates when slicks were oriented parallel to shore[1]					
	4 June 1985			21 August 1985		
	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]	Slicks $n = 3$	Ripples $n = 3$	Slicks/ ripples[2]
Total fish	12±2.9	4.2±0.9	3*	1.7±0.9	0.8±0.3	2
Hypsoblennius hentzi	6.0±2.1	3.1±0.2	2	0.1±0.1	0.4±0.1	0.3
Membras martinica	1.7±1.1	0.3±0.1	5	0	0	—
Hyporhamphus unifasciatus	0.7±0.7	0.6±0.4	1	0	0	—
Brevootia tyrannus	1.6–0.8	0	—	0	0	—
Monacanthus hispidus	0.9±0.6	0	—	0.8±0.6	0	—
Cheilopogen heterurus	0	0	—	0.2±0.1	0	—
Miscellaneous	1.1±0.3	0.3±0.2	4	0.4±0.4	0.2±0.1	2
Total Brachyura	41±12	1.7±0.6	24*	12±3.9	0.5±0.4	22*
Callinectes spp.						
Megalopa	0.2±0.2	0	—	3.9±1.7	0.2±0.1	19*
First crab	1.5±0.6	0	—*	0.2±0.2	0	—
Portunus spp.						
Megalopa	36±11	1.6±0.8	23*	7.5±21	0.3±0.3	24*
First crab	1.2±0.6	0	—	0	0	—
Miscellaneous	2.0±1.1	0.1±0.1	15*	0.3±0.2	0	—
Amphipods	40±16	1.2±0.1	33*	2.2±1.5	0	—
Polychaete larvae	5.2±1.7	0.7±0.5	8*	0	0	—
Stomatopod larvae	0	0	—	32±8.8	8.1±2.6	4*
Cnidaria	0	0	—	9.9±2.9	18±6.2	1
Salpa	0	0	—	15±2.6	60±2.9	0.3*
Sargassum floats	11±6.8	0.8±0.6	14*	8.8±1.4	0.4±0.3	21*

	Dates when slicks were oriented perpendicular to shore								
	14 July 1985			20 July 1985			21 August 1985		
	Slicks $n = 3$	Ripples $n = 3$	Slicks ripples[2]	Slicks/ $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]	Slicks $n = 4$	Ripples $n = 4$	Slicks/ ripples[2]
Total fish	2.6±0.4	0.9±0.5	3*	1.2±0.3	1.0±0.2	1	1.1±0.1	1.8±1.0	1
Hypsoblennius hentzi	0	0	—	0.6±0.2	0.8±0.1	1	0.3±0.2	1.5±0.9	0.2
Hyporhamphus unifasciatus	0.5±0.3	0	—	0.4±0.2	0	—	0	0	—
Monacanthus hispidus	0	0.2±0.2	0	0	0	—	0.3±0.2	0.2±0.2	2
Cheilopogen heterurus	1.0±0.4	0	—	0	0	—	0.2±0.2	0	—
Miscellaneous	1.2±0.4	0.4±0.4	2	0.1±0.1	0.2±0.8	1	0.4±0.3	0.2±0.2	3
Total Brachyura	3.6±1.3	5.2±0.9	1	0.9±0.3	0.3±0.3	3	1.6±0.5	0.6±0.4	3
Callinectes spp.									
Megalopa	0.4±0.3	0.6±0.6	1	0.4±0.2	0	—	0.2±0.2	0	—
Portunus spp.									
Megalopa	0.9±0.6	2.2±0.6	0.4	0.2±0.2	0.2±0.2	3	0.1±0.1	0.3±0.3	0.5
Miscellaneous	1.8±0.7	2.2±0.1	1	0.1±0.1	0.2±0.2	1	1.4±0.5	0.3±0.2	5
Amphipods	5.7±3.9	2.9±0.6	2	4.4±0.7	1.7±0.8	3	0	0	—
Polychaete larvae	18±7.3	8.1±5.2	2	0	0	—	2.6±1.3	0.3±0.2	8
Stomatopod larvae	0	0	—	0	0	—	9.9–1.5	9.1±2.6	1
Cnidaria	83±15	126±73	1	0	0	—	7.8±1.2	4.9±1.7	2
Salpa	91±36	103±78	1	0	0	—	239±35	130±38	2
Sargassum floats	22±16	3.6±1.7	6	0.4±0.1	0.1±0.1	5	5.2±2.4	1.1±0.3	5

[1]Also included in this category are the data from 24 June (Tables 2 and 4).
[2]The ratio of the abundance in the slick divided by the abundance in the rippled water. * = $P \leq 0.5$ Wilcoxon's two-sample test (Sokal and Rohlf 1969).

Ocypoda spp. are abundant in neuston net tows (Smyth 1980; Johnson 1985a). Juvenile filefish, *Monacanthus hispidus*, are abundant in neuston tows (Fahay 1975; Eldridge et al. 1977) and are commonly found associated with floating seaweeds (Dooley 1972). Larval *Hyporhamphus unifasciatus* and *Hypsoblennius hentz* are abundant in surface plankton tows (Fahay 1975; Eldridge et al. 1977; Fritzsche 1978). Both their behavior (Breder and Clark 1947) and abundance in neuston tows (Eldridge et al. 1977) suggest that larval *Sphoeroides maculatus* are also residents of the surface waters. These results suggest that there is an assemblage of larvae unique to the neuston and that tests of the

internal-wave-mediated larval transport hypothesis outlined in the introduction can be made.

The distribution of organisms followed a pattern similar to that of Sargassum floats (Tables 1, 2, 4). In the tows from internal waves oriented perpendicular to shore there was only one instance in which the density of an organism was significantly higher in the convergence than the divergence zone (total larval fish, 14 July 1985, Table 1) indicating that these internal waves were not transporting larvae.

TABLE 2.—The density (mean no./100 m^2 ± SE) of invertebrates and Sargassum floats in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test.

	Density Mean no./100 m^2 ± SE, n = 3					Significance[1]		
Species	In front	Internal wave[2]	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Total Brachyura	1.1±0.2	6.5±1.3	21±5.7	2.5±0.2	0.2±0.2	*	*	*
Portunus spp.								
Megalopa	0.3±0	3.8±0.9	14±4.2	0.8±0.2	0	*	*	*
First crab	0	1.2±0.7	4.7±2.5	0.1±0.1	0		*	*
Callinectes spp.								
Megalopa	0.2±0.2	0.2±0.1	0.9±0.2	0	0.1±0.1		*	
Miscellaneous								
Megalopa	0.6±0.3	1.7±0.3	1.8±0.7	1.7±0.2	0.1±0.1			
Amphipods	30±8.1	176±112	754±546	0.3±0.3	20±6.5		*	
Polychaete larvae	2.9±1.1	16±3.0	62±8.6	2.5±1.3	1.8±0.6		*	*
Penaeus spp.								
Postlarvae	1.8±1.3	34±6.5	94±6.5	16±4.4	0.4±0.4		*	*
Sargassum floats	0.9±0.1	42±29	182±122	0.6±0.3	0	*	*	*

[1]Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P \leq 0.05$.
[2]Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = [(slick no./m^2 × 30 m^2) + (ripples no./m^2 × 100 m^2)/130 m^2] × 100.

TABLE 3.—Comparison of the density of various types of megalopae and larval fish caught in neuston, oblique, and bottom plankton tows.

	Density, no./100 m^2						
	14 June 1985		9 June 1986		19 June 1986 Mean ± SE, n = 3		
Species	Neuston	Oblique	Neuston	Oblique	Neuston	Oblique	Bottom
Crab megalopa							
Portunus spp.	0	0	0	0	5.3±4.5	0	0
Callinectes spp.	0	0	0	0	3.1±2.4	0	0
Ocypoda quadrata	0	9.0	0	0	1.5±1.4	0	0
Pinnotheridae	0.4	9.0	0	9.0	0.1±0.1	310±160	18.7±9.2
Xanthidae	0	88.8	0	9.0	0	690±250	17.0±9.6
Cancer spp.	0	0	0	0	0	66.7±40.6	1.4±0.8
Unknown and misc.	2.0	239	0.2	90.0	1.3±0.8	194±89.2	11.4±3.6
Fish larvae							
Monacanthus hispidus[1]	0	0	1.1	0	0.1±0.1	0	0
Hyporhamphus unifasciatus[1]	0	0	0	0	0.3±0.2	0	0
Sphoeroides maculatus	0	0	0	0	0.3±0.1	0	0
Membras martinica	0.4	0	0	0	0	0	0
Hypsoblennius hentzi	0	0	0	0	0.3±0.3	6.0±6.0	0
Symphurus plagiusa	0	44.4	0	27.0	0	190±60	0.1±0.1
Prionotus evolans	0	18.0	0	136	0	510±210	15.1±6.0
Seriola spp.	0	0	0	27.0	0	46.0±17.8	0.3±0.3
Engraulidae	0	18.0	0	217	0	280±99	16.2±8.9
Unknown and misc.	0	9.0	2.2	63.0	0	150±110	3.9±3.0

[1]Juvenile or late postflexion stages only.

TABLE 4.—The density (mean no./100 m^2 ± SE) of larval fish in front of the set of internal waves, the weighted average over the internal waves, in the internal wave slick (convergence zone), the rippled water between slicks (divergence zone), and behind the internal waves. Significance compares the density between these samples using a Wilcoxon's two-sample test. J = Juvenile, LPF = Late Post Flexion, EPF = Early Post Flexion, F = Flexion, PF = Preflexion, and Total = Sum of all stages.

	Density Mean no./100 m^2 ± SE, n = 3					Significance[1]		
Species	In front	Internal wave	Slicks	Ripples	Behind	In front vs. behind	Slicks vs. ripples	In front vs. internal wave
Monacanthus hispidus	1.1±0.1	2.0±0.4	8.1±9.0	0.2±0.2	0.1±0.1		*	*
Hyporhamphus unifasciatus								
J	0	0.1±0.1	0.2±0.9	0	0			
LPF	0.1±0.1	0.9±0.5	4.2±2.3	0	0			*
EPF	0	0.5±0.2	1.8±0.6	0	0		*	*
F	0	0.1±0.1	0.2±0.2	0	0		*	
PF	0	—	0	0	0			
Total	0.1±0.1	1.5±0.6	6.5±2.6	0	0		*	*
Membras martinica								
J	0	0.1±0.1	0.4±0.4	0	0			
LPF	0	—	0	0	0			
EPF	0	—	0	0	0			
F	0	0.1±0.1	0.5±0.3	0	0			
PF	0.2±0.1	0.2±0.1	14±4.2	0.4±0.4	1.0±0.6		*	*
Total	0.2±0.1	0.2±0.1	15±44	0.4±0.4	1.0±0.6		*	*
Hypsoblennius hentzi								
J	0	0.2±0.2	0.8±0.8	0	0			
LPF	0	0.2±0.1	0.5±0.3	0	0		*	
EPF	0	0.2±0.0	0.7±0.1	0	0		*	*
F	0.3±0.9	0.2±0.1	0.9±0.4	0	0		*	
PF	14±2.4	4.5±1.8	16±6.0	0.9±0.5	2.6±0.2	*	*	
Total	14±2.0	5.2±1.6	19±5.5	0.9±0.5	2.6±0.2	*	*	
Brevoortia tyrannus								
F	0.2±0.1	0.1±0.1	0.5±0.3	0	0.2±0.2			
PF	0.7±0.2	0.2±0.1	0.6±0.3	0	0.1±0.1			
Total	0.9±0.3	0.2±0.0	1.1±0.1	0	0.4±0.4			
Miscellaneous								
J	0	0.5±0.2	1.8±0.9	0	0		*	*
LPF	0	0.2±0.1	0.8±0.9	0	0.1±0.1		*	*
EPF	0	—	0	0	0			
F	0.1±0.1	0.1±0.1	0.4±0.4	0	0			
PF	0	0.1±0.1	0.4±0.4	0	0			
Total	0.1±0.1	0.8±0.2	3.4±1.0	0	0.1±0.1		*	*
Grand total	16±1.6	13±1.0	53±3.6	1.6±0.2	4.2±0.4	*	*	

[1]Wilcoxon's two-sample test (Sokal and Rohlf 1969). * = $P < 0.05$.
[2]Weighted average density over an internal wave assuming a 30 m wide slick and a 100 m wide ripples. Internal wave = [(slick no./m^2 × 30 m^2) + (ripples no./m^2 × 100 m^2)/130 m^2] × 100.

In contrast, in tows from internal waves oriented parallel to shore there were numerous instances in which larval densities were significantly higher in the slicks (Tables 1, 2, 4); the densities observed in the slicks were 4- to >50-fold higher than those in the rippled waters. These data demonstrate that a variety of larval and postlarval invertebrates and fish were transported shoreward by these internal waves.

On 24 June 1985, surface plankton samples were collected in the first two slicks over a set of internal waves oriented parallel to the shore, in the rippled water between these slicks, and in front and behind the entire set of internal waves. Ninety-six percent of the surface drifters were caught by the first two convergence zones and carried shoreward about 4 km. The density of Sargassum floats was highest in the slicks (>100-fold, Table 2) and they were at significantly lower densities behind the set of internal waves than in front. There were 0.9 Sargassum floats/100 m^2 in the waters in front of the set of internal waves and none in the waters

behind the waves (Table 2). The distribution of tar balls (spilled asphalt) over and around the internal waves was similar to the distribution of Sargassum floats (Shanks 1987). As these internal waves propagated shoreward, the currents over the waves swept buoyant flotsam from the waters in front of the set of waves into the convergence zone where the flotsam was caught and carried shoreward.

Calculation of the density of larvae or flotsam over the internal waves (i.e., density in the slicks plus the ripples) requires knowledge of the width of the slick and rippled waters over the internal waves. Unfortunately, in this initial study these measurements were not made, necessitating that these widths be approximated using values from the literature. Slicks were assumed to be 30 m wide and the rippled waters separating the slicks were assumed to be 100 m wide. These values are consistent with my experience and with published values (LaFond 1959; Sawyer 1983). The observed density over one internal wave was calculated as (slick no./m^2 × 30 m) + (ripples no./m^2 × 100 m)/130 m^2. The density over an internal wave was compared with the density in an equal area of water in front of the set of internal waves. Making these calculations for Sargassum floats gives an observed density of 42 floats/100 m^2 over the internal wave vs. 0.9 floats/100 m^2 in front of the set; the density over the internal wave is significantly larger (46-fold greater) than the density in front of the set (Table 2). Again the data indicate that Sargassum floats were carried shoreward by the internal waves.

None of the types of larval fish characteristic of water column samples (Table 3) were caught in any neuston tow. Present in the neuston tows were only those types of larval and juvenile fish which my samples and the descriptions in the literature suggest are characteristically neustonic.

The densities of larval and juvenile fish frequently were significantly higher in the slick samples than the samples from the rippled waters between slicks (Table 4). On 24 June 1985, most larval fish, especially juvenile and postflexion stage larvae, were rare in both the waters in front and behind the set of internal waves. On this date in 6 tows, 3 in front and 3 behind the set of internal waves, only 4 juvenile and postflexion larvae were caught as compared to 185 in the 3 tows made in the slicks. Probably because of the rarity of larval fish in both in front and behind tows there were only three cases, total and preflexion *Hypsoblennius hentz* and total larval fish, in which the density of fish in front of the set of internal waves was significantly higher than behind the set (Table 4). There are seven instances, however, in which the density over the internal wave of a larval or juvenile fish was significantly and at least 10-fold higher than the density in front of the set of internal waves (Table 4). In six of these instances the fishes were at the juvenile, late postflexion, or early postflexion stages of development.

Larval and juvenile fish were grouped by stage of development and the densities over and in front of the internal waves were calculated for each developmental stage (Fig. 2). The densities over the internal waves of the juvenile, late postflexion, and early postflexion developmental stages were significantly higher than the densities of these stages in front of the set. There was not a significant difference between the densities over and in front of the set of internal waves of flexion stage larvae and preflexion larvae were significantly more abundant in front of the set. These data suggest that internal

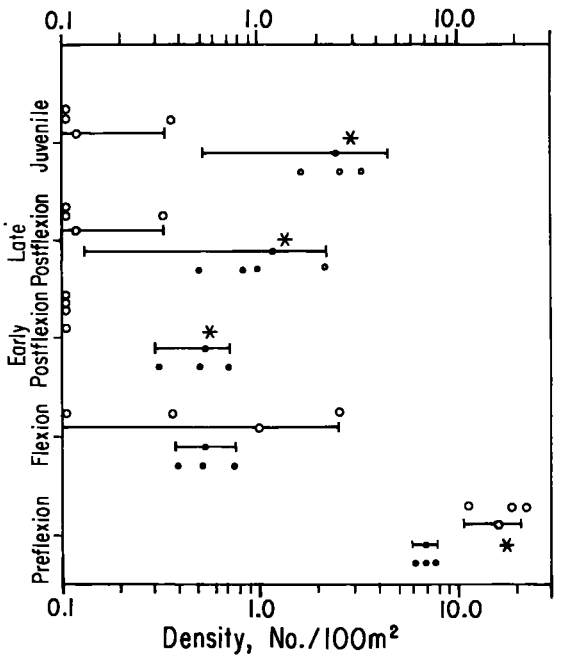

FIGURE 2.—Densities of larval fish by stage of development caught on 24 June 1985 in the waters in front of the set of internal waves (open circles) and over the internal waves (closed circles). Data are presented as the mean ±95% confidence interval with the points above or below this line being the actual observations. Asterisks indicate cases where the in front density was significantly different (Wilcoxon's two-sample test, $P \leq 0.05$) from the density over the internal waves. The method of calculating the densities is described in the text.

waves are capable of carrying fish larvae shoreward, but shoreward transport seems to be confined to postflexion stage larval or juvenile fish.

In the samples from 24 June 1985 there are a number of cases in which a fish species and/or stage of development was common in the tows from the convergence zones but was absent or very rare in the divergence zones, in front, or behind the set of waves (i.e., zero or one caught in the nine tows from these three habitats, Table 4). Either these larval fish are extremely rare in the waters surrounding the internal waves in which case the convergence zone must have accumulated larvae from a large volume of water or the internal waves transported the larvae into the study area from a distant source.

On 24 June 1985, the density of total Brachyura was significantly higher in the slicks over the internal waves than in any other area sampled (Table 2). *Portunus* spp., a group which previous data had demonstrated inhabited the neuston, made up the bulk of the Brachyura caught. The densities of *Portunus* were significantly higher in the slicks than the rippled water between slicks. The density of *Portunus* spp. megalopae differed significantly from 0.3/100 m^2 in front of the set of internal waves to 0/100 m^2 behind (Table 2). *Portunus* spp. first crabs were absent from both the waters in front and behind the set of internal waves; they were abundant in the waters over the internal wave (Table 2). The densities over the internal waves of *Portunus* spp. megalopae and first crabs were significantly higher than their densities in front of the set of waves (Table 2). *Callinectes* spp. were uncommon in the samples though their density was significantly higher in the slick than in the rippled waters. Included under the category of miscellaneous megalopae were the species *Uca* spp., *Sesarma* spp., and majid crabs, all forms which were found to be more abundant in the water column than in the neuston (Table 2). There was not a significant difference between their density in the slicks vs. the rippled waters, suggesting that these megalopae were not carried shoreward by the sampled set of internal waves. The data indicate that definitely *Portunus* spp. and possibly *Callinectes* spp. were carried onshore by the sampled set of internal waves.

Other organisms counted in the samples were adult amphipods, polychaete larvae, and *Penaeus* spp. postlarvae. Densities of these types of organisms were significantly higher in the slicks than the rippled waters (Table 2). While in each instance densities were lower behind the set of internal waves than in front, the differences were not statistically significant. The density of polychaete larvae and *Penaeus* spp. postlarvae over the internal waves were significantly higher than the density in front of the set. These data suggest that these invertebrate larvae were also transported onshore by the set of internal waves.

DISCUSSION

Tidally generated internal waves have been observed in many areas of the world (Apel et al. 1975; Fu and Holt 1982; Sawyer 1983). Larvae may utilize internal waves as a mechanism of onshore migration along many coastlines. Testing this hypothesis would require the impossible task of making observations along all coastlines. An alternate technique is to test for internal wave transport in areas with different combinations of tidal range and shelf width. Previous work has been done in areas of mesotides (tidal range 2 to 4 m, Davis 1964) and either narrow (<6 km, Shanks 1983) or moderate (about 30 km, Kingsford and Choat 1986) shelf widths. The Atlantic adjacent to the Beaufort Inlet is characterized by microtides (tidal range <2 m, Davis 1964) and a wide shelf (about 80 km). The first purpose of this research was to test if onshore transport of larvae could occur in an area with these characteristics. On the three dates in which the internal-wave-slicks were oriented roughly parallel to shore the data suggest that internal waves were transporting larvae and flotsam onshore. If the waters around the Beaufort Inlet are representative of localities with microtides and wide shelves, then onshore migration of larvae via internal waves may occur in other similar areas of the world.

On three dates the internal-wave-slicks were oriented nearly perpendicular to shore and were propagating roughly northward. Over the continental shelf, internal waves oriented roughly perpendicular to shore have been observed in satellite photographs. These internal waves are invariably associated with submarine canyons (Apel et al. 1976). There are no submarine canyons in Onslow Bay. The internal waves causing these slicks may have been formed over Frying Pan Shoals (Fig. 1). These shoals extend about 50 km across the shelf from the end of Cape Fear and form the southern boundary of Onslow Bay. Just north of the study area, Cape Lookout and the Cape Lookout Shoals also extend out across the shelf (Fig. 1). On a flight over Cape Lookout numerous slicks oriented parallel to Cape Lookout Shoals were observed propagating northward into Rayleigh Bay (pers. obs.). The geography

and oceanography of the Cape Lookout and Frying Pan Shoals are so similar that by analogy the internal waves oriented perpendicular to shore observed during this study may have been formed over Frying Pan Shoals and propagated northward into Onslow Bay. The mechanism for the formation of these internal waves is unknown.

As was observed in a previous study (Shanks 1983), only some sets of internal waves transported larvae or flotsam. In this study only those slicks aligned parallel to shore caused transport. It is not clear why some sets of waves cause transport while others do not. The physical characteristics of tidally generated internal waves are quite variable. The amplitude (Cairns 1968) and decay distance of internal waves varies over the fortnightly tidal cycle (Brink 1988). Further, the depth, wave length, and shape of the internal waves is dependent on the relative depths of the thermocline and the bottom and wave amplitude (LaFond 1959; Lee 1961; Cairns 1967, 1968). What is needed is simultaneous measurements of the physical characteristics of a set of internal waves much like those made by LaFond (1959) with measurements of the transport of flotsam or larvae.

The second purpose of this research was to test several new predictions derived from the hypothesis that internal waves can transport larvae. If transport was occurring, then one would predict that 1) due to the accumulation of larvae in the convergence zones as internal waves propagate shoreward, the density of larval types transported by the internal waves should be significantly lower behind than in front of the set, 2) the observed density of larvae over an internal wave should be significantly higher than in the waters in front of the set of waves, and 3) there may be types of larvae which are only present in the slicks, suggesting that they had been carried into the area from a distant source. The appropriate samples to test these three predictions were collected on 24 June 1985. The densities of several larval types were significantly higher in the waters in front of the internal wave set than behind. There were many instances in which the observed density over the internal waves of a type of larvae was significantly higher than in the waters in front of the set of internal waves. Lastly, there were a number of organisms that were only caught in the convergence zones over the internal waves. In this set of observations the three predictions were confirmed indicating that this set of internal waves was carrying larvae and flotsam shoreward.

The significant differences in larval densities observed on 24 June (i.e., in front vs. behind and over the internal waves vs. in the front of the set of waves) may have been due to fortuitous cross-shelf patchiness in larval density. Because conditions allowed only one opportunity to sample in front and behind a set of internal waves, this alternate explanation can not be rejected. Cross-shelf larval patchiness is, however, probably not an adequate explanation because of the very short distance over which large differences in larval abundances were observed. For example, the tows in front of the set and the tows in the slick and rippled water over the set were separated by at most 200 m, yet there were many cases (14, Tables 2, 4) where larval abundances were different by at least a factor of 10. Differences in plankton abundance of this magnitude and over this small a distance are almost always associated with oceanographic features (e.g., fronts: Boden 1952; Pingree et al. 1974; Owen 1981; Fogg et al. 1985). The only apparent oceanographic feature in the study area was the internal-wave-slicks. The observed differences in larval density were probably caused by the internal waves.

The data in Figure 2, the density of fish by stage of development over the internal waves vs. in front of the set of waves, suggest that only the later developmental stages of fish (juvenile through early postflexion) were transported onshore by the set of internal waves sampled on 24 June 1985. All five of the abundant fish species (Table 4) inhabit near shore or estuarine habitats as adults (Fritzsche 1978; Hardy 1978; Johnson 1978; Martin and Drewry 1978). Flexion and preflexion larval fish are clearly not competent to adopt the adult or nursery habitat, and the data suggest that they were not carried onshore by the internal waves. There may be adaptive advantages to planktonic larvae avoiding estuarine waters during their development (Strathmann 1982). Juvenile fish and, perhaps, also postflexion larvae, are competent to recruit into the adult or nursery habitat. Transport onshore by internal waves may, therefore, be adaptively advantageous for those fish whose adult or nursery habitat is coastal or estuarine.

The larval development of the blue crab, *Callinectes sapidus*, occurs at sea (Smyth 1980; McConaugha et al. 1983; Johnson 1985b). The larvae are present in the waters over the continental shelf and out to the Gulf Stream (Smyth 1980). At the end of the larval period the megalopae must return to an estuarine habitat to continue its adult existence. How the megalopae make this migration is an open question (Johnson et al. 1984; Johnson

1985b). The behavior of the megalopae (Sulkin and Van Heukelem 1981) and their distribution in the plankton (Smyth 1980; Johnson 1985a) both suggest that these larvae are inhabitants of the neuston. Larvae that inhabit the neuston can be transported onshore by internal waves (Shanks 1985). On 4 and 24 June and 21 August the densities of *Callinectes* spp. megalopae and first crabs were significantly higher in the convergence zones over the internal waves than in the divergences, suggesting that *Callinectes* spp. were being transported onshore by the sampled internal waves. On 24 June, when *Callinectes* spp. were uncommon, there was not a significant difference in the density of *Callinectes* spp. in front vs. behind the internal wave nor was there a significant difference in the density of blue crabs over vs. in front of the set of waves. These results are mixed, but they do suggest that the megalopae of *Callinectes* spp. may be transported shoreward in the convergence zones over internal waves.

The megalopae of a variety of crab species were only caught in the water column (Table 3 and see Johnson 1985a). Some of these megalopae as adults occupy near shore and even estuarine habitats. If these megalopae migrate onshore they must be utilizing some mechanism of onshore transport other than slicks over internal waves.

In conclusion, the data presented in this paper indicate that in an area where the tides are of small amplitude and the continental shelf is wide, internal waves are nevertheless capable of transporting larval invertebrates and fish shoreward. The samples collected on 24 June 1985 more critically test the hypothesis that internal waves cause cross-shelf transport and the results support the hypothesis.

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TROPHIC RELATIONS OF THE BLUE ROCKFISH, *SEBASTES MYSTINUS*, IN A COASTAL UPWELLING SYSTEM OFF NORTHERN CALIFORNIA

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ABSTRACT

The planktivorous *Sebastes mystinus* in nearshore habitats off northern California feeds primarily on relatively large, gelatinous zooplankters that originate offshore, including thaliaceans, ctenophores, and pelagic hydrozoans. These prey organisms increase in number during spring and summer when surface waters driven seaward by northerly winds carry upwelled nutrients to diatoms that nourish offshore zooplankton populations. But the resulting increases in zooplankton during this upwelling season become available to *S. mystinus* in the nearshore habitats only when the surface flow turns shoreward during intermittent episodes of downwelling. Although some of this shoreward flow is driven by southerly winds, much of it occurs during calms, or under northerlies lacking the velocities needed to drive surface waters seaward. There is increasing shoreward transport during fall and winter, when downwelling episodes are more frequent, but progressively fewer zooplankters are carried into the nearshore habitats. This is because as less nutrients come into the system with the reduced upwelling, and as available sunlight declines, the offshore zooplankton populations suffer from shortages of diatoms. Although *S. mystinus* compensates for decreased numbers of zooplankters during most of the year with increased consumption of specific plant materials, i.e., *Nereocystis sori*, or the monostromatic epiphytes *Porphyra nereocystis* and *Smithora naidum* (depending on the season), these too are in short supply during winter. In winter, therefore, *S. mystinus* experiences its poorest feeding conditions. Thus, *S. mystinus* is adapted to feeding opportunities created by alternating episodes of strong upwelling and strong downwelling, and is most abundant within its range along the west coast of North America where both conditions are well developed.

Coastal marine fishes in temperate latitudes experience major seasonal changes in their environment. In study off northern California's Mendocino coast (lat. 39°13'N, long, 123°14'W), we studied the effects of seasonal change on the trophic relations of the blue rockfish, *Sebastes mystinus* (Fig. 1). *Sebastes mystinus*, a major species in the recreational fishery off northern and central California (Frey 1971), is a planktivore that feeds on scyphozoans, ctenophores, copepods, amphipods, thaliaceans, fishes, and algae (Gotshall et al. 1965; Love and Ebeling 1978; Hallacher and Roberts 1985). Although its diet is known to vary with the season, relationships involving specific environmental features, and the availability of prey, remain unclear.

The marine environment off California is profoundly affected by seasonal variations in wind-driven movement of the surface water (Reid et al. 1958; Bolin and Abbott 1962; Bakun and Parrish 1980). This force, known as Ekman transport (Ekman 1905), is strongest off the Mendocino coast (Bakun 1973), where it must be a major influence on the trophic relations of *S. mystinus*. Because Ekman transport is the basis of coastal upwelling (e.g., Smith 1968), it is of great importance to biological productivity (e.g., Boje and Tomczak 1978) and, therefore, to the availability of food.

Upwelling develops along the coast of northern California when surface waters driven seaward by northerly winds, such as those characteristic of spring and summer, are replaced by colder subsurface waters from offshore that flow up into the nearshore habitat (Smith 1968; Bakun 1973). On the other hand, an opposing condition develops when surface waters driven shoreward by southerly winds, such as those characteristic of winter storms, flow over the colder nearshore waters to produce the condition sometimes called downwelling (Bakun 1973). But despite the strong seasonality evident in both upwelling and downwelling, short-term reversals lasting just a few days occur throughout the year (see Bakun [1973] and Mason and Bakun [1986]).

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FIGURE 1.—*Sebastes mystinus* next to canopy of bull kelp, *Nereocystis leutkeana*, off Mendocino.

In this paper we consider how the trophic relations of *S. mystinus* respond as seaward and shoreward movements of the surface water produce alternating episodes of upwelling and downwelling. Emphasis is on how the resulting environmental changes alter the relative availability of food. Among studies of marine fishes, this is, to our knowledge, the most comprehensive attempt yet made to integrate data on food, potential food, and environmental variables—all key elements in trophic relations.

METHODS

The study lasted from the winter of 1976–77 to the summer of 1981, with the first 15 months involving exploratory work along about 15 km of the Mendocino coast south of Point Cabrillo. A study site was then established off Salmon Point (Fig. 2) during the spring of 1978, and from that time sampling followed a set regime.

Study Site

The study site (Fig. 3) was in 10–15 m of water, about 300 m from shore. Rocks the size of houses jutted 10–15 m above the water at the seaward perimeter of the site, but despite the shelter offered by these rocks, most of the area was regularly swept by wind and sea. Except for isolated pockets of sand, the site was floored by rock pavement and boulders (some 5–15 m in diameter), largely swept clean by the turbulence and surge that prevailed most of the time.

Environmental Variables

During each sampling session, we noted the gen-

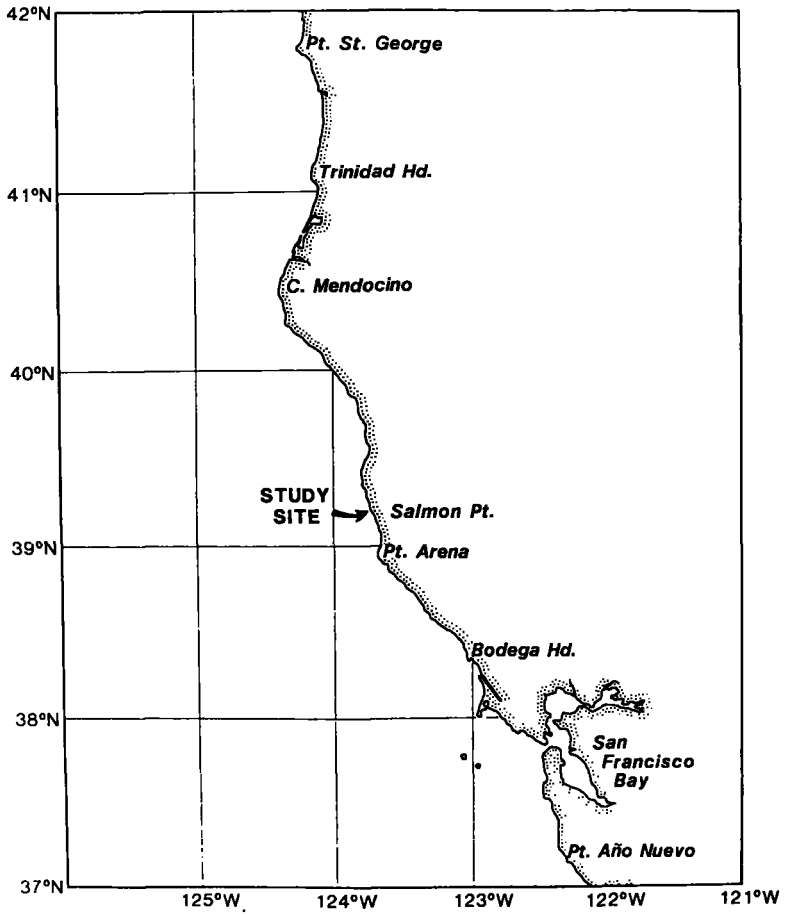


FIGURE 2.—The coast of northern California.

eral state of the weather, including wind direction and estimated velocity. In this paper (except in Figures 4 and 9, as noted below) we consider winds from between northwest and northeast to be "northerly", and from between SW and SE to be "southerly". We also noted sea conditions and recorded sea-surface temperatures. More precise wind data became available after May 1980, when a NOAA weather station was established at Mendocino. During the same month, we placed recording thermographs at depths of 6 and 20 m in the study area, and although the deeper site was abandoned after 1981 in favor of replicating the record with two instruments at the shallower site, these have given us a continuous record of water temperatures from then until the present (Spring of 1988). Based on these observations and in situ visual assessments of the plankton and water characteristics, usually we could tell whether upwelling or downwelling predominated during a sampling session even though most of the time conditions were to some extent mixed.

Diet and Occurrences of Food

To relate the diet of *S. mystinus* to foods present at the time of feeding, we took concurrent samples of gut contents and plankton, as well as some selective samples of the benthos. Complications from normal diel variability were reduced by taking all samples between the hours of 1100 and 1300. The sampling schedule was strongly influenced by the weather, as much of the time work was prevented by high seas and/or long-period swells and result-

FIGURE 3.—Study site off Salmon Point.

ing turbulence. Although all seasons were sampled, most collections and observations were made when the sea was relatively calm, a condition that generally lasted no more than a few days at a time. Nevertheless, because often the weather turned while observations were under way, turbulent conditions were well represented.

Fish

The *S. mystinus* studied at Mendocino were spatially segregated by size and age. This paper considers only adult fish of more than 200 mm SL, which forage by day in aggregations of up to several hundred individuals in the upper levels of the water column. The analysis of gut-contents involved 247 individuals, 200–350 mm SL, taken from these aggregations using handheld spears. Juveniles and subadults are excluded because they forage at lower levels of the water column and consume organisms not taken by adults.

Plankton

Most sampling sessions included two plankton collections: one at the sea surface, and the other between 1 and 2 m above the sea floor. Only the 27 surface collections are considered here, however, because the others sampled at levels of the water column below where adults usually feed. For each collection we used scuba to push the net (0.333 mm mesh in a 78 cm × 78 cm frame) through the water for 5 minutes. Occasionally the net broke the surface, but usually was kept underwater to avoid fouling the sample with floating debris. (See Hobson and Chess 1976 for additional information on this pro-

cedure, and how the samples were processed and analyzed.) We visually assessed the larger zooplankters in the water column during each collection, as well as at other times during each sampling session, and these observations greatly enhanced our ability to interpret the samples.

Benthos

Although *S. mystinus* is a planktivore, it is important to include the benthos when documenting environmental changes that affect its feeding. Many of the actual or potential foods of *S. mystinus* originate on the underlying substrata, and their occurrences in the water column relate to changes in the benthos. Thus, assessments of the benthos done during other studies concurrently under way in the study area, including visual counts and airlift samples, produced data that are incorporated into this report where pertinent.

Ranking Prey Taxa

To estimate the relative importance of the various prey organisms in the diet of *S. mystinus*, we grouped related forms in multispecies categories that were then ranked. The ranking was based on an index calculated as: relative frequency of occurrence in diet × mean number of individuals consumed × percent of total diet volume that was represented by that category. This index is similar to the widely used Index of Relative Importance (IRI) of Pinkas et al. (1971), but puts more weight on numbers consumed. It is important to emphasize numbers consumed in quantifying the feeding activity of *S. mystinus* (and most other planktivores) because the many small prey are ingested individually, making the capture of each a discrete act.

RESULTS

During the four years of this study, spring and (to a lesser extent) summer constituted an upwelling season, while fall and (to a greater extent) winter constituted a downwelling season. The spring transition between downwelling and upwelling seasons occurred over just a few days between late March and early April, whereas the less distinct fall transition between upwelling and downwelling seasons was extended over a month or more between mid-August and late October.

Despite this seasonal pattern, however, there were short-term reversals of just a few days that had profound effects. Reactions of the environment to major wind changes were virtually immediate. Sharply reduced water temperatures signifying the intrusion of upwelled water often followed within hours of increased northerly winds, while warmer water rich in such readily visible zooplankters as ctenophores, hydrozoans, pteropods, thaliaceans, and larvaceans, often flowed into the nearshore habitats within a day after the onset of southerly winds. Conditions during each sampling session are listed in Table 1.

Although downwelling conditions were most intense under southerly winds, they also developed during calms and with weak northerlies. We found that generally it took northerlies of 10 knots (K) or more to produce upwelling conditions, although as little as 5 K were effective if held steady for several days. In the absence of sufficient force, however, upwelling ceased and warmer water rich in offshore zooplankters entered the nearshore habitat, generally moving in a southerly direction along the coast.

The close relation between shifts in prevailing wind and alternations between upwelling and downwelling is illustrated by comparing the wind direction and velocity measured by the nearby NOAA weather station to the sea temperatures recorded by our thermographs. Although these data became available only during the last year of the study, subsequent years have produced similar profiles (except 1982–83, when there was a strong El Niño). Thus, the pattern of sea temperatures and wind during the upwelling season of 1981 and during the downwelling season of 1980–81, recounted in detail below, are representative.

The Upwelling Season

The upwelling season began in late March or early April with a precipitous drop in sea temperatures. It was a drop of about 3°C—typically from 11°–12°C to 8°–9°C—that coincided with the onset of strong, persistent northerly winds characteristic of this time of year. The pattern of sea temperatures and wind during the 1981 upwelling season (Fig. 4) illustrates how upwelling and downwelling related to prevailing winds during that period.

Habitat Conditions

At the start of the upwelling season, the nearshore habitats appeared barren. Storm seas during the previous winter had carried away most of the bull

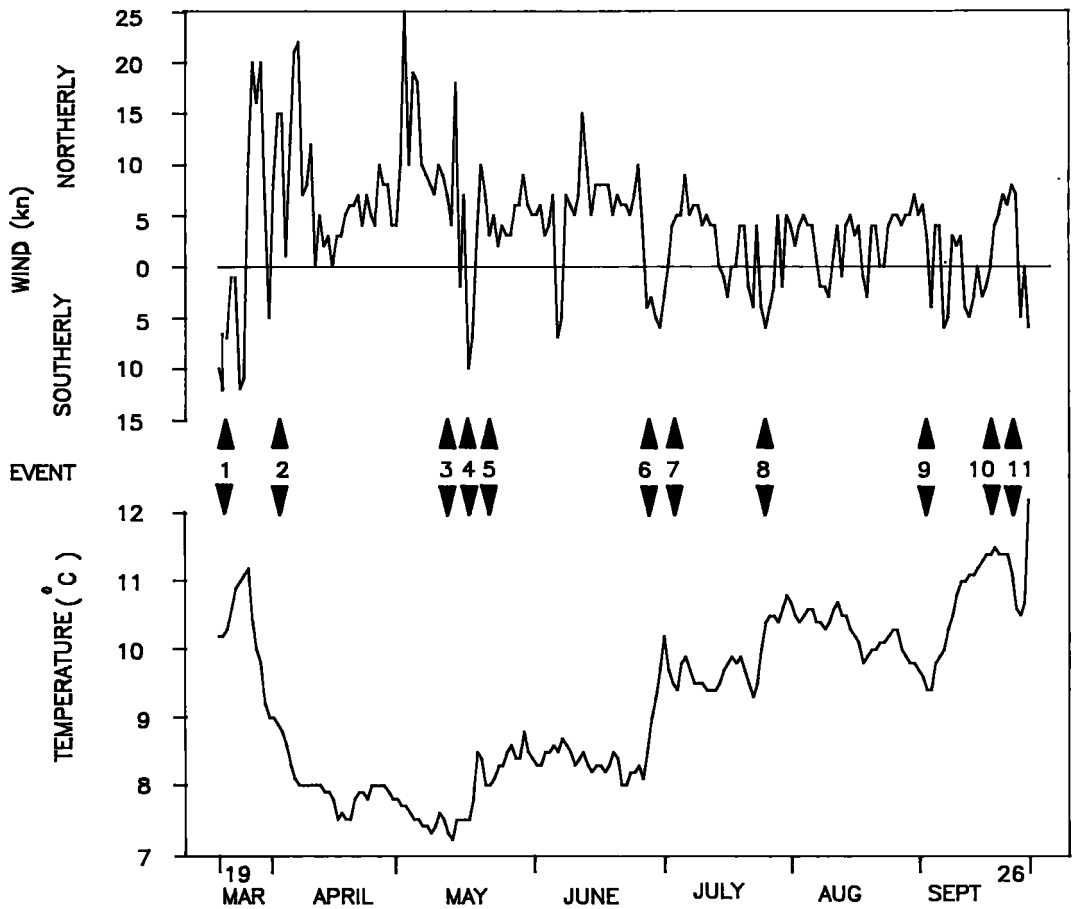


FIGURE 4.—Sea temperatures and wind off Mendocino during the 1981 upwelling season. *Plotted sea temperatures* are estimated daily means from record of continuously recording thermograph. Plotted wind velocities and directions are averages of 2–5 daily readings. Southerly values represent winds from south of east-west axis, northerly values represent winds from north of this axis. The highly infrequent winds from due west or due east were entered as zero. In calculating values for days of both northerlies and southerlies, the former were considered positive, the latter negative. The following accounts of events identified in the figure cite wind velocities that exceed plotted values, which are averages.

EVENT 1—Seven days of southerly winds, 19–25 March, with sea temperatures rising to 11.1°C, represented the last downwelling episode of the 1980–81 downwelling season.

EVENT 2—The 1981 upwelling season began on 26 March, as 2 weeks of strong northerlies (to 4 April) resulted in an abrupt drop of more than 3°C in sea temperature.

EVENT 3—Water temperatures fell to the lowest point of the year, 7.3°C, on 13 May following over 2 weeks of 10–30 K northerlies.

EVENT 4—The first of a series of downwelling episodes during this upwelling season developed as 8–12 K southerlies on 17 and 18 May resulted in a sharp rise in sea temperature to 8.5°C.

EVENT 5—Temperatures dipped when the wind shifted back to the north on 19 May. Over the next month variable northerlies blew at less than 10 K, and although sea temperatures did not vary more than a few tenths of a degree, they were consistently about 1°C warmer than before the 17–18 May downwelling episode.

EVENT 6—On 28 June, the first of 6 consecutive days of 4–10 K southerlies, sea temperatures began a steep climb to above 10°C that marked the upwelling season's second major downwelling episode.

EVENT 7—Northerlies returned on 3 July, and sea temperatures immediately dropped below 10°C again. Despite northerlies of 5–7 K over the next 2 weeks, sea temperatures remained at about 9.5°C, again about 1°C warmer than before the 28 June–2 July downwelling episode.

EVENT 8—With southerlies of 5–10 K on 7 of the 9 days between 12 and 20 July, sea temperatures once again rose above 10°C to mark the season's third major downwelling episode.

TABLE 1.—Conditions during sampling sessions off Salmon Point, Mendocino County, 1978–81.

Date	Sea temp. (°C)	Wind dir. : vel. (knots)	Plankton condition[1]	Fish sampled No.	Size range (mm)	Mean (mm)
I. Upwelling season, upwelling conditions						
5/10/78	8.5	NW: 10	U/M	7	270–312	289.7
8/08/78	10.5	NW: 10	U	6	285–309	293.0
6/12/79	9.0	NW: 15	U/M	7	241–312	239.3
6/24/80	10.0	None	U	9	224–308	250.0
4/09/81	8.1	NW: 15	U	8	235–300	265.6
5/19/81	9.5	WNW: 10	U/M	1	260	260.0
6/17/81	9.0	NNW: 10	U	13	260–336	301.0
II. Upwelling season, downwelling conditions						
6/21/78	9.0	None	D/M	3	228–308	270.3
6/29/78	10.0	SW: 2	D/M	6	240–315	254.7
8/23/78	11.0	None	D	6	230–280	259.0
9/08/78	14.0	None	D	4	240–295	277.5
4/24/79	10.0	None	M	9	225–313	277.7
7/24/79	11.5	None	M	11	208–302	239.5
8/27/79	12.8	NW: 5	M	12	204–335	264.6
5/29/80	9.5	None	D/M	20	213–330	276.4
7/17/80	11.0	NW: 5	D/M	5	240–304	270.8
8/21/80	11.0	S: 5	D	9	230–305	270.6
III. Downwelling season, downwelling conditions, fall						
10/04/78	11.0	WNW: 10	D+	3	270–310	286.7
10/18/78	12.0	S: 5	D+	9	220–350	296.2
12/08/78	9.0	S: 8	D+	17	227–331	281.2
10/16/79	14.0	NW: 8	D	13	218–311	280.1
11/04/80	12.0	N: 6	D	17	230–335	296.6
12/17/80	12.0	NNW: 5	D	14	225–331	276.3
IV. Downwelling season, downwelling conditions, winter						
2/04/79	10	S: 12	D	12	231–320	273.3
3/06/79	11	W: 8	D	2	224–260	242.0
1/31/80	11	None	M	16	200–345	275.3
1/13/81	13	SW: 5	D	8	275–305	286.3

[1]Plankton condition. D = Downwelling condition: zooplankters considered to be offshore species, especially relatively large gelatinous forms, numerous. U = Upwelling condition: offshore zooplankters absent. M = Mixed condition: some offshore zooplankters present.

kelp, *Nereocystis leutkeana*, which is the major component of the kelp forests. These same seas, often heavily laden with sediment, had also scoured the seafloor of much of the algal understory, as well as many of the sedentary invertebrates. Once the upwelling season had been established, however, the habitats changed rapidly.

Often during early-season upwelling the water was relatively transparent, although after rains visibility often was limited by suspended sediment discharged into the nearshore habitat from coastal streams. By mid-May, however, the numbers of planktonic diatoms (primarily *Chaetoceros* sp. and *Nitzchia* sp.) had greatly increased to depths of

EVENT 9—In the last major upwelling of this upwelling season, sea temperatures fell to 9.4°C on 2 September after 10 consecutive days of 5–8 K northerlies.

EVENT 10—Sea temperatures rose steadily to 11.4°C on 17 September after 1–3 day periods of 4–8 K northerlies had alternated with 1–4 day periods of 4–8 K southerlies through the first half of that month.

EVENT 11—Sea temperatures fell to 10.5°C on 24 September after 7 consecutive days of 5–15 K northerlies. A shift to southerlies on 25 September started another climb, and the transition to the downwelling season clearly was under way. This transition, however, was not nearly so well defined as that which had introduced the upwelling season 6 months before.

10–20 m, which often limited visibility to a few meters. These diatom blooms were most evident during the intermittent episodes of downwelling. The benthos similarly proliferated. Within a few weeks after the initial upwelling, a growth of benthic diatoms (primarily *Isthmia nervosa* and *Tricertium americana*) appeared on the previously baron rocks, and even on sand sheltered from wave surge. Then larger elements of the biota began to increase in size and number. Particularly evident were calcareous sponges (especially *Leucosolenia* spp.), hydroids, and certain bryozoans. Benthic algae, predominantly *Desmarestia ligulata*, rapidly overgrew much of the rock substrata, while young *Nereocystis leutkeana*, which first appeared on the seafloor in May, had grown to the water's surface by mid-June. Swarms of mysids were increasingly numerous near the seafloor in April (they had been prominent for a month or more), and caprellid and gammaridean amphipods on rocky substrata began a sharp increase in numbers.

The bull kelp had formed a dense canopy by mid-July, and at about the same time large numbers of sori (reproductive structures) began falling from the kelp's fronds. (A frond that had recently lost a sorus appears at the left side of Figure 1.) Planktonic diatoms continued to proliferate during periodic blooms, but by this time the benthic diatoms that had carpeted much of the seafloor during the spring were mostly gone. Similarly, the mysid swarms, which had peaked in May and June, usually began to decline by mid-July. Other elements of the biota,

TABLE 2.—Food of adult *Sebastes mystinus* relative to near-surface plankton during upwelling episodes of the upwelling season. n = 7.

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	PLANTS (3751.20)	**NR[2]**	**72**	**NR**	**52.1**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	15–20	15	1.10	10.6	NR	NR	NR	NR
	Porphyra sp.	NR	15	NR	9.9	NR	NR	NR	NR
	Smithora naidum	NR	21	NR	17.0	NR	NR	NR	NR
	Others	NR	21	NR	14.6	NR	NR	NR	NR
2	PELAGIC HYDROZOA (1373.30)	**10–30**	**21**	**4.51**	**14.5**	**<1–4**	**86**	**120.08**	**2.3**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	<1–2	86	68.65	0.6
	Syphonophora								
	Muggiaea atlantica	—	0	0.00	0.0	—	0	0.00	0.0
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	3–4	14	51.43	1.7
	Chondrophora								
	Velella velella	10–30	21	4.51	14.5	NA[3]	NA	NA	NA
3	MYSIDACEA (203.15)	**5–7**	**3**	**10.26**	**6.6**	**—**	**0**	**0.00**	**0.0**
	Acanthomysis spp.[4]	5–7	3	10.26	6.6	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
4	SCYPHOZOA (61.60)[5]	**NR**	**8**	**NR**	**7.7**	**NR**	**NR**	**NR**	**NR**
	Fragments	NR	8	NR	7.7	NR	NR	NR	NR
5	EUPHAUSIACEA (35.10)	**5–8**	**15**	**1.95**	**1.2**	**<1–4**	**57**	**363.60**	**3.1**
	Larvae	—	0	0.00	0.0	<1–4	57	363.60	3.1
	Thysanoessa spp.	5–8	15	1.95	1.2	—	0	0.00	0.0
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	GAMMARIDEA (1.80)	**1–8**	**8**	**0.75**	**0.3**	**1–8**	**86**	**10.31**	**5.3**
	Atylus tridens	—	0	0.00	0.0	2–8	29	4.63	5.0
	Ishyrocerus n. sp.	4	3	0.31	0.1	—	0	0.00	0.0
	Jassa falcata[6]	1–3	8	0.28	0.1	<1–3	14	0.78	NR
	Polycheria osbourni	—	0	0.00	0.0	—	0	0.00	0.0
	Others	2–8	5	0.16	0.1	1–2	57	4.90	0.3
7	CALANOIDA (0.90)	**5–6**	**8**	**0.16**	**0.7**	**<1–7**	**100**	**2454.09**	**38.6**
	Nauplii	—	0	0.00	0.0	<1	14	72.00	0.1
	Acartia spp.	—	0	0.00	0.0	1–2	52	224.23	4.4
	Calanus pacificus	—	0	0.00	0.0	2–3	57	24.68	5.3
	Eucalanus californicus	6	8	0.13	0.6	4–7	71	35.48	1.4
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others[7]	5	3	0.03	0.1	<1–3	1	2097.70	27.4

however, reached maximum development during the summer. Prominent among them were benthic algae, e.g., *Desmarestia ligulata* and *Laminaria setchelli*, as well as certain sedentary animals including various sponges, e.g., *Leucilla nuttingi*; ascidians, e.g., *Tridid emnum opacum*; hydroids, e.g., *Obelia* spp.; and bryozoans, e.g., *Bugula* spp. The benthic caprellids and gammarideans attained peak numbers during early summer, when they literally carpeted some areas of the seafloor. Samples taken with an airlift during July 1978 measured densities of over 10,000 caprellids (mostly *Metacaprella kennerleyi*), and 108,000 gammarids (mostly *Jassa* spp.) in m^2 quadrats. Their numbers declined sharply during August, however, and by September they occurred only in scattered patches.

Feeding Conditions

The diet of *S. mystinus* relative to foods present during the upwelling season was assessed with samples of gut contents and near-surface plankton taken during 7 upwelling episodes (Table 2) and 10 downwelling episodes (Table 3).

More prey were consumed during the downwelling episodes (e.g., $\bar{x}$ no. prey taken = 110.8, vs. 20.1 during upwelling episodes). Thaliacians (Fig. 6) were the primary food during the upwelling season, but all were taken during downwelling episodes—the only times when the guts were packed with food. These relatively large, gelatinous zooplankters did not occur either in the plankton or in the diet of *S. mystinus* during upwelling episodes.

TABLE 2.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	CAPRELLIDEA (0.54)	**10**	**5**	**1.08**	**0.1**	**6**	**14**	**2.25**	**0.4**
	Metacaprella kennerlyi	10	5	1.08	0.1	—	0	0.00	0.0
	Others	—	0	0.00	0.0	6	14	2.25	0.4
9	CHAETOGNATHA (0.09)	**23**	**3**	**0.03**	**1.0**	**3–12**	**57**	**20.80**	**2.1**
	Undetermined species	23	3	0.03	1.0	3–12	57	20.80	2.1
10	FISHES (0.02)	**12**	**3**	**0.05**	**0.1**	**2–14**	**57**	**14.92**	**1.1**
	Larvae	12	3	0.05	0.1	2–14	57	14.92	1.1
OTHER CATEGORIES									
	Polychaeta	—	0	0.00	0.0	<1–12	86	74.83	1.4
	Molluscan larvae	—	0	0.00	0.0	<1–1	57	149.92	1.7
	Pelagic gastropoda	—	0	0.00	0.0	1–5	29	2.32	8.6
	Cladocera	—	0	0.00	0.0	1	29	64.28	0.7
	Harpacticoida	—	0	0.00	0.0	1–2	1	54.77	0.7
	Cyclopoidea	—	0	0.00	0.0	1	71	75.08	0.9
	Cirripedean larvae	—	0	0.00	0.0	<1–1	1	1850.92	15.0
	Reptantian larvae	—	0	0.00	0.0	<1–2	86	134.48	1.9
	Natantian larvae	—	0	0.00	0.0	2–3	43	72.00	1.4
	Larvacea	—	0	0.00	0.0	3–8	43	53.48	1.1
	Eggs, undetermined	—	0	0.00	0.0	<1	43	3024.00	9.7
	Eggs, fish	—	0	0.00	0.0	<1–2	71	312.68	1.7
UNIDENTIFIABLE MATERIAL[8]		—	—	—	15.9	—	—	—	—
No. fish examined: 51 224–336, $\bar{x}$ = 284.3 mm SL No. empty = 13 $\bar{x}$ no. prey: individuals = 20.13 taxa = 2.03						No. plankton collections: 7 $\bar{x}$ no. zooplankters: 4940.57			

[1]Value is estimated mean number per 100 m^3 of water, based on water filtered (54.8 m^3) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[4]Most mysids sampled were *Acanthomysis sculpta*.
[5]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata* (Fig. 5), which were avoided by us during plankton collections because they would have made collections unmanageable.
[6]According to Kathleen Conlan (National Museum of Canada, P.O. Box 3443, Station D, Ottawa, Canada K1P 6P4, pers. commun. 26 May 1987), *Jassa falcata* does not occur in California, and forms along the coast considered to be this species (including the form(s) referred to here) are undescribed.
[7]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[8]Foods digested beyond recognition.

FIGURE 5.—Adult *Sebastes mystinus* feeding on a scyphozoan, *Cyanea capillata*.

TABLE 3.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of the upwelling season. n = 10.

Food organism		In diet				In plankton			
Rank	Taxa (rank index)	Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
1	THALIACEA (124990.86)	**1–10**	**47**	**76.20**	**34.9**	**3–45**	**30**	**130.70**	**8.9**
	Undetermined species	1–10	47	76.20	34.9	3–45	30	130.70	8.9
2	PLANTS (2030.40)	**NR[2]**	**54**	**NR**	**37.6**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	18	NR	9.7	NR	NR	NR	NR
	Porphyra sp.	NR	22	NR	11.5	NR	NR	NR	NR
	Smithora naidum	NR	15	NR	5.5	NR	NR	NR	NR
	Others	NR	28	NR	10.9	NR	NR	NR	NR

TABLE 3.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
3	**CALANOIDA (778.78)**	**3–6**	**20**	**16.93**	**2.3**	**<1–8**	**100**	**5557.10**	**31.9**
	Nauplii	—	0	0.00	0.0	<1–1	50	594.00	1.8
	Acartia spp.	—	0	0.00	0.0	1–2	1	1121.00	4.6
	Calanus pacificus	—	0	0.00	0.0	2–5	70	105.84	2.4
	Eucalanus californicus	4–6	20	16.92	2.3	1–8	70	796.68	14.6
	Rhincalanus nasutus	—	0	0.00	0.0	5–6	10	92.88	2.7
	Others[3]	3	1	0.01	<0.1	<1–3	1	2846.70	5.8
4	**HYPERIIDEA (405.13)**	**2–13**	**49**	**6.36**	**1.3**	**1–7**	**60**	**17.10**	**0.6**
	Hyperoche medusarum	2–6	5	0.38	0.1	1–7	20	9.72	0.3
	Vibilia spp.	5	24	4.35	0.7	—	0	0	0
	Others	2–13	23	1.63	0.5	1–3	40	7.38	0.3
5	**PELAGIC GASTROPODA (334.66)**	**1–20**	**16**	**5.81**	**3.6**	**1–18**	**20**	**37.44**	**1.1**
	Heteropoda								
	Caranaria japonica	10–20	8	2.35	2.0	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	10–15	11	3.45	1.6	15–18	10	4.32	0.8
	Limacina helicina	3	1	0.01	<0.1	1–2	20	33.12	0.3
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	**PELAGIC HYDROZOA (318.24)**	**2–35**	**30**	**1.56**	**6.8**	**1–20**	**70**	**240.66**	**8.8**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	10–20	10	0.54	0.3
	Others	—	0	0.00	0.0	1–5	50	187.56	5.8
	Syphonophora								
	Muggiaea atlantica	8–9	5	0.27	0.2	6–9	10	2.88	0.6
	Stephanomia bijuga	NR	5	0.31	0.2	—	0	0.00	0.0
	Others	2–16	14	0.51	2.7	2–6	20	49.68	2.1
	Chondrophora								
	Velella velella[4]	25–35	7	0.47	3.7	NA[4]	NA	NA	NA
7	**LARVACEA (1.12)**	**2–7**	**8**	**0.70**	**0.2**	**2–6**	**70**	**142.74**	**2.2**
	Undetermined	2–7	8	0.70	0.2	2–6	70	142.74	2.2
8	**POLYCHAETA (0.87)**	**4–25**	**19**	**0.46**	**0.1**	**<1–7**	**70**	**103.50**	**0.7**
	Larvae	—	0	0.00	0.0	<1–4	70	90.36	0.3
	Postlarvae	4–25	19	0.46	0.1	7	10	13.14	0.4
9	**FISHES (0.73)**	**8–45**	**4**	**0.14**	**1.3**	**2–11**	**50**	**4.50**	**0.4**
	Larvae	8–45	4	0.14	1.3	2–11	50	4.50	0.4
10	**SCYPHOZOA (0.02)**	**NR**	**3**	**0.01**	**0.5**	**NR**	**NR**	**NR**	**NR**
	Fragments	NR	3	0.01	0.5	NR	NR	NR	NR
OTHER CATEGORIES									
	Molluscan larvae	NR	1	0.01	<0.1	<<1–<1	70	631.08	4.9
	Cladocera	—	0	0.00	0.0	<<1–<1	40	115.92	1.7
	Harpacticoida	NR	3	0.03	NR	<1–2	70	55.25	1.1
	Cirripedean larvae	—	0	0.00	0.0	<1–2	100	1372.44	11.8
	Gammaridea	1–8	12	0.32	0.5	<1–3	90	12.24	0.6
	Euphausiacea	2–12	9	0.11	0.7	<1–11	60	229.86	1.0
	Reptantian larvae	—	0	0.00	0.0	<1–3	70	119.52	2.1
	Natantian larvae	—	0	0.00	0.0	1–6	60	43.20	0.7
	Chaetognatha	—	0	0.00	0.0	6–18	50	18.54	1.2
	Eggs, undetermined	NR	12	0.74	0.3	<<1–<1	50	2921.40	5.0
	Eggs, fish	—	0	0.00	0.0	<1–2	60	48.96	0.9
UNIDENTIFIABLE MATERIAL[5]		—	—	—	11.0	—	—	—	—

No. fish examined: 85
204–335, $\bar{x}$ = 266.2 mm SL
No. empty = 8
$\bar{x}$ no. prey: individuals = 110.84
taxa = 3.35

No. plankton collections: 10
$\bar{x}$ no. zooplankters: 6622.50

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]NR = not recorded. The enumeration was either omitted or unfeasible.
[3]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Foods digested beyond recognition.

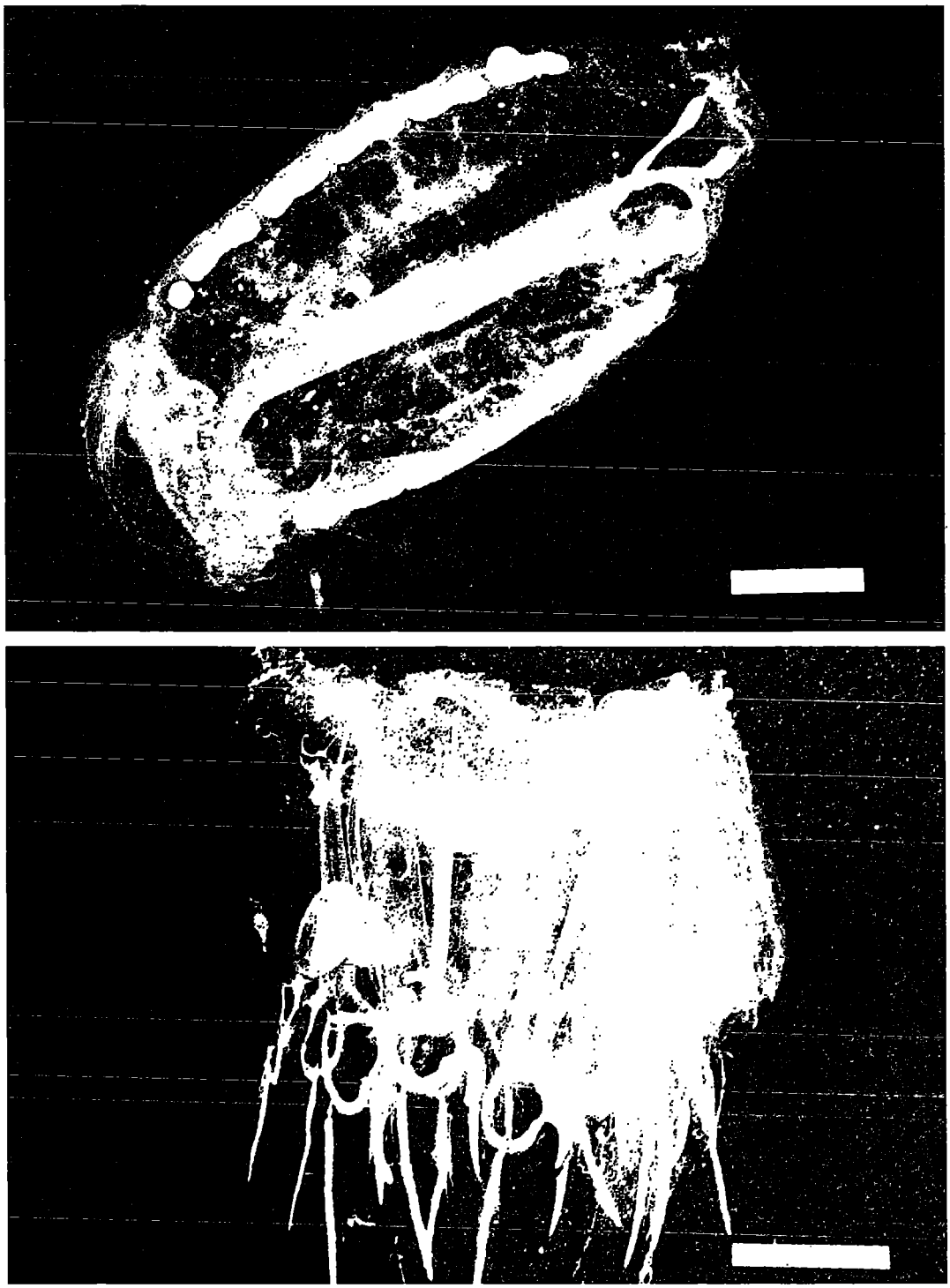


FIGURE 6.—Thaliacean, *Cyclosalpa bakeri*, off Mendocino. Solitary individual (upper) and aggregate of individuals (below). Scale indicator = 1 cm.

Plant material ranked as the top food-category during upwelling episodes (Table 2) and as the second-ranked food during downwelling episodes (Table 3). In both cases, certain algae dominated the diet on days when offshore zooplankters were in short supply during the latter part of the upwelling season (upwelling episodes on 8 August 1978, 12 June 1979, and 17 June 1981; downwelling episodes on 24 July 1979 and 27 August 1979; see Table 1). Algae were not taken earlier in the season, however. Thus, while the six individuals collected during a plankton-poor upwelling episode of 8 August 1978 (Table 1) were full of algae (90% of gut contents) and epibenthic crustaceans (10%), all eight collected during a plankton-poor upwelling episode of 9 April 1981 (Table 1) were empty. Similarly, the occurrence of algae in the diet during downwelling episodes (Table 3) is based mostly on 20 adults collected during two days (24 and 27 August 1979) when environmental conditions indicated downwelling but an absence of offshore zooplankters was noted (Table 1). There was no indication of plants being ingested for epiphytic animals.

Of the wide variety of plant materials in the diet, only the three most frequently ingested forms appeared to some extent digested. These were the sori of *N. leutkeana*, *Porphyra nereocystis* (an epiphyte on *N. leutkeana*), and *Smithora naidum* (an epiphyte on certain seagrasses). The sori of *N. leutkeana* developed as variably sized areas (typically about 50–150 mm long) in fronds near the water's surface. They dropped from the fronds when mature, and we saw several ingested by *S. mystinus* as they drifted toward the bottom. Sori recovered from the intestines of *S. mystinus* were more translucent than sori from the stomach, but comparison under magnification of sectioned material from both regions of the gut (Fig. 7) indicated that only zoospores were digested. Ingested fragments of *P. nereocystis* and *S. naidum*, both species having monostromatic thalli, ranged from intact, but flaccid and blanched, to disintegrating. Ingested *S. naidum* often were attached to pieces of *Zostera marina* or *Phyllospadix torreyi*, but these seagrasses never evidenced digestion. Nor did other plant forms present among the gut contents appear to be digested, including *D. ligulata* and *N. leutkeana* (vegetative tissue), along with various unidentified phaeophytes and rhodophytes. Thus, plants contributed less food than is indicated by the tables and histograms, where their rank is inflated by undigested materials.

Zooplankters taken during upwelling episodes differed from early to late in the season, whereas those taken during downwelling episodes remained much the same throughout (as listed in Table 3). Thus, of the food categories listed for the upwelling condition (Table 2), pelagic hydrozoans, mysids, and scyphozoans were taken only during the spring, whereas euphausiids and caprellids were taken only in summer. The only notable departure from the downwelling condition depicted in Table 3 occurred on 24 April 1979 (Table 1), when conditions were at the time judged to be mixed. Upwelling had been unusually weak during the first month of that upwelling season, and there was no wind at the time of sampling. The sea was calm and, at 10°C, warm for April. Although these conditions usually indicate downwelling (which is why the data are assigned to that category), we neither collected nor saw organisms typical of downwelling conditions. Furthermore, of the nine adult *S. mystinus* (224–313, $\bar{x}$ = 277.7 mm SL) collected, eight (89%) were empty. The ninth contained one sorus from *N. leutkeana* (an unusually large number of *N. leutkeana* had persisted through the previous winter, which had been exceptionally mild) and also organisms not seen or collected by us in the environment at the time: two *Corolla spectabilis* (a pelagic gastropod typical of downwelling conditions) and six *Velella velella* (a pelagic hydrozoan typical of upwelling conditions). The latter float on the water's surface (Fig. 8), and often we saw adult *S. mystinus* break the surface to feed on them.

The Downwelling Season

Between late August and mid-September it became evident that transition to the downwelling season was under way. Winds had become light and variable (but generally remained either northerly or southerly), and for a growing number of days at a time, the water was notably blue and transparent. Records of sea temperatures and wind for the 1980–81 downwelling season illustrate how occurrences of downwelling and upwelling related to prevailing wind during that period (Fig. 9).

Habitat Conditions

The downwelling season developed with less wind from the north and more wind from the south, but either way with winds that tended to be light, so that relatively tranquil conditions prevailed. Flowing into the nearshore habitat with offshore surface waters was a rich supply of relatively large, mostly gelatinous zooplankters that were major prey of *S.*

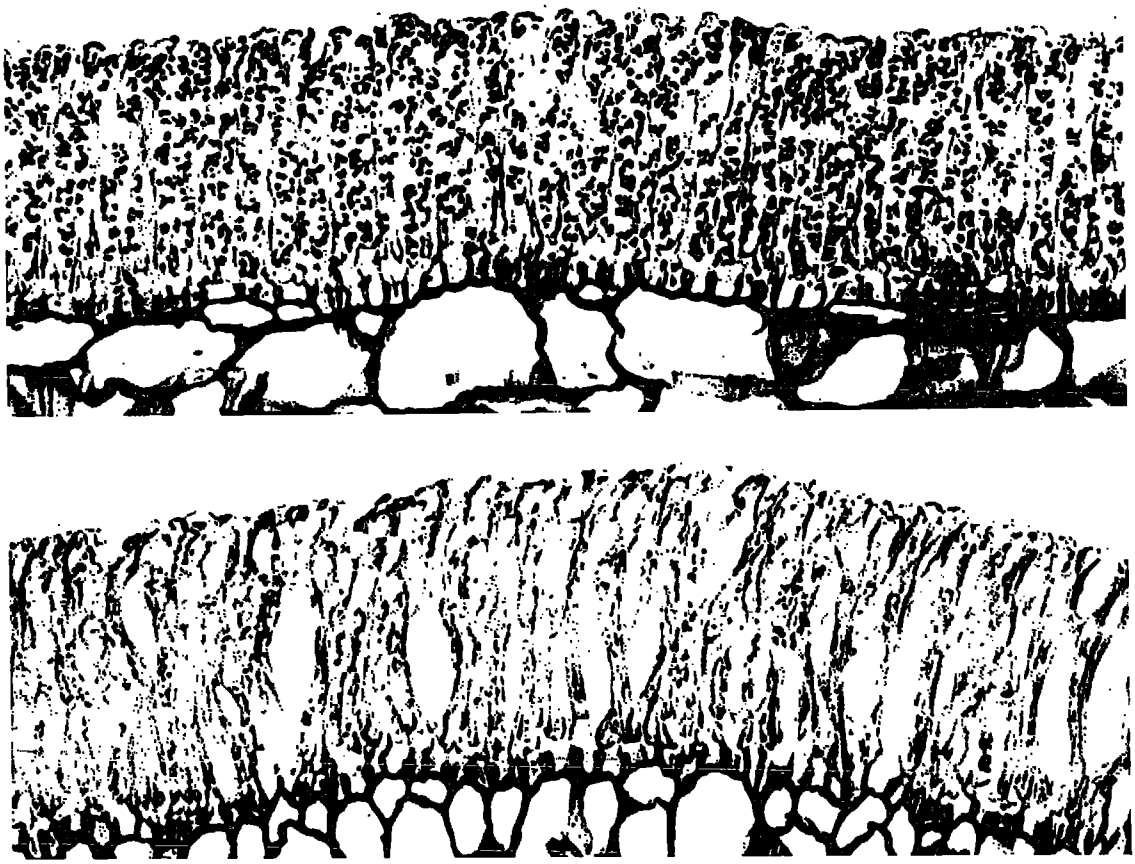


FIGURE 7.—Sections through surface region of sori (stained with hematoxylin) from gut of *Sebastes mystinus*. Upper section is from the stomach, lower is from the intestine. Granular objects in upper section but largely absent in lower section are zoospores in zoosporangia.

mystinus. But, whereas the predominant of such forms during spring and summer usually were thaliaceans, during the fall they were usually ctenophores (Fig. 10), pelagic hydrozoans—mostly siphonophores (Fig. 11), and hydromedusae. The pelagic hydrozoan *Velella velella*, which had been prominent during the upwelling season, was not seen. Pelagic gastropods (Fig. 12), pteropods at least, also were more abundant during fall downwelling. On the other hand, these waters were poor in the pelagic diatoms that had bloomed periodically during spring and summer. Furthermore, the nearshore habitat had by this time lost much of its benthos. Many of the more insecurely anchored *Nereocystis* plants, for example, had been carried away by strong wave surge that frequently swept through the nearshore habitat even during relatively tranquil periods. Although the loss of these plants greatly increased interplant distances, *Nereocystis* beds remained dominant features. This was because the plants still in place continued to grow, to produce sori, and to thicken the surface canopy. Probably at least partly because the canopy's increased thickness blocked sunlight from the seafloor below, the algal understory, *Desmarestia lingulata* in particular, was greatly reduced. Similarly, many benthic animals that proliferated during the previous upwelling season had become scarce, including the amphipods and mysids noted above to be declining during late summer.

As the downwelling season progressed through fall toward winter, there were major transformations of the nearshore habitat that, to at least some extent, resulted from southwesterly storms. The

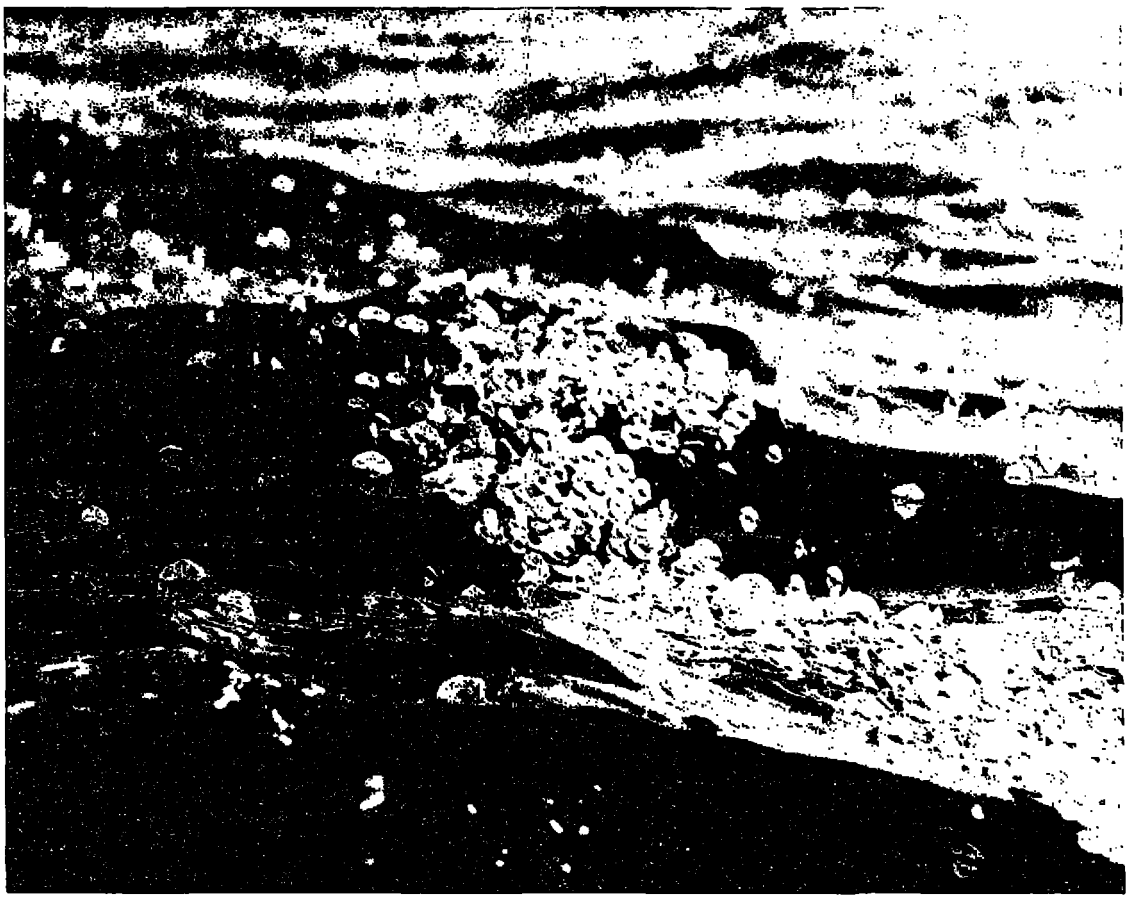


FIGURE 8.—*Velella velella* being driven shoreward by a northwest wind off the coast of northern California.

major effects of storms on the nearshore habitats came from 1) physical force of waves and surge, and 2) suspended sediments carried by coastal runoff into the nearshore habitats after heavy rains. The first of these was the more apparent, at least in exposed locations where often many of the benthic algae and sessile invertebrates were swept away. This force, intensified when the water carried abrasive sediments, swept away most of the *Nereocystis*, although some plants survived the winter in sheltered places where they continued to produce sori. Suspended sediments had their most obvious effects in locations sheltered from water movement, where they frequently settled to blanket the benthos. Probably a more profound effect of materials in suspension, however, was reduced transparency of the water that limited the amount of light (already at low levels owing to the shorter days and low sun angle) reaching phototrophic organisms.

As a general result of these, and probably other forces in combination, the nearshore habitat appeared relatively barren during the latter stages of the downwelling season. That storms were a major factor in reducing the vitality of this habitat was apparent during the relatively mild winter of 1978–79, when the effects described above were reduced. That was the only year, for example, when mysids were noted to be conspicuous in the nearshore habitat throughout the winter.

Feeding Conditions

The diet of *S. mystinus* relative to foods available during the downwelling season was assessed during 10 days of sampling under downwelling condi-

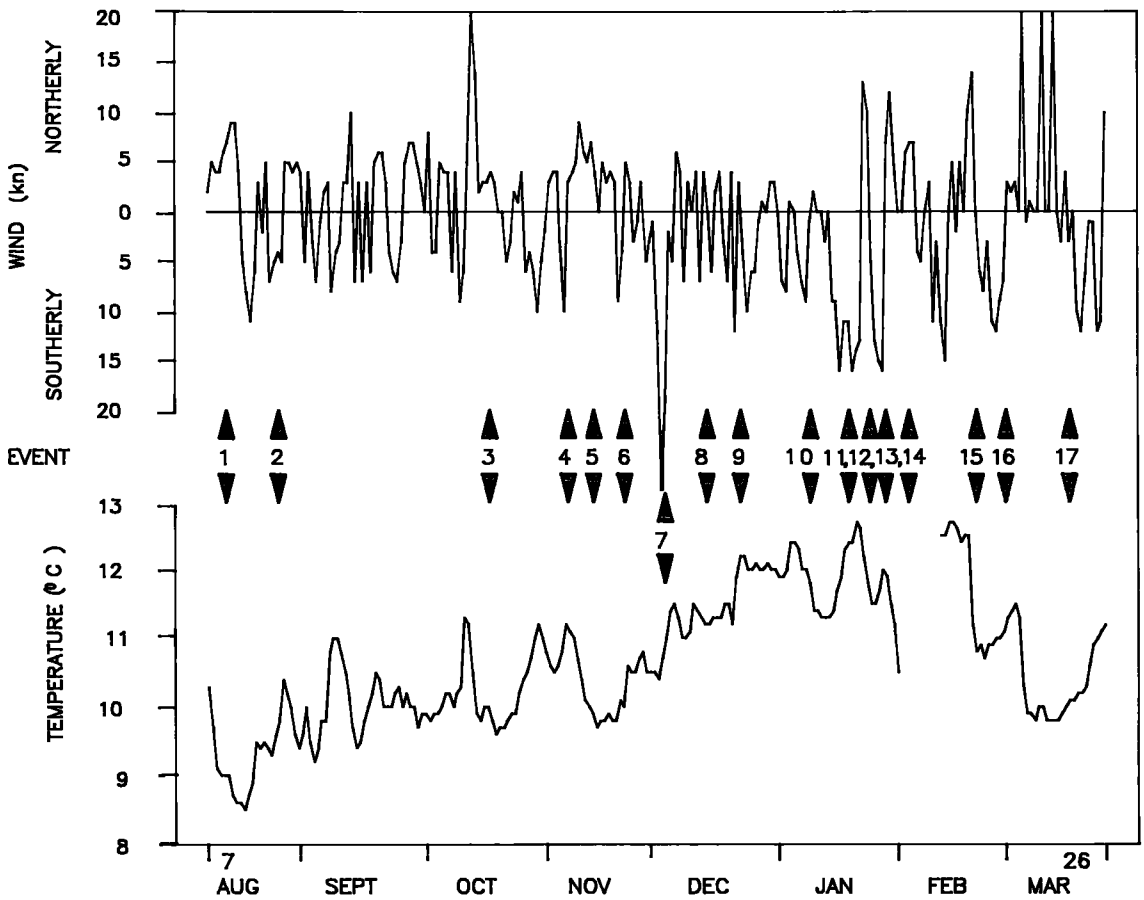


FIGURE 9.—Sea temperatures and wind off Mendocino during the 1980–81 downwelling season. See capture of Figure 4 and text for methods used in obtaining and plotting the data.

EVENT 1—Sea temperature fell to 8.5°C on 16 August after 9 consecutive days of 7–10 K northerlies, producing the last episode of strong upwelling during the 1980 upwelling season.

EVENT 2—Sea temperature rose to 10.4°C on 26 August after southerlies of 5–12 K on 9 of the preceding 11 days. Then began a 6-wk transition to the downwelling season, during which 1–4 day periods of 2–10 K northerlies, with slightly lowered sea temperatures, alternated with 1–4 day periods of southerlies, with slightly elevated temperatures.

EVENT 3—The last bit of upwelling before the season's first major downwelling episode began on 14 October with 7 consecutive days of northerlies—20 K during the first 2, 4–8 K during the next 5.

EVENT 4—Sea temperatures rose to 11.2°C on 7 November after 16 straight days of 2–12 K southerlies or weak (2–5 K) northerlies.

EVENT 5—Sea temperatures fell to 9.7°C during a major cooling that coincided with 8 days of 3–9 K northerlies (with gusts to 20 K) from 8 to 15 November.

EVENT 6—On 21 November the wind shifted to the south, with gusts to 20K, and sea temperatures began rising.

EVENT 7—A 3-day storm (1–3 December) with 20–30 K southerlies (and rain) briefly accelerated the rise in temperature.

EVENT 8—The warming trend was briefly interrupted by several 1–3 day periods of 4–10 K northerlies.

EVENT 9—By 22 December sea temperatures had risen to levels above 12°C that characterized the 1980–81 downwelling season. Although southerlies predominated over the next 3 weeks, on some days reaching 25 K (e.g., on 25 December), there were no further large increases in temperature.

EVENT 10—Sea temperatures anomalously fell during the first 2 weeks of January, even though winds during that period were mostly southerlies of up to 10 K.

EVENT 11—An 8-day storm (15–22 January) with 12–20 K southerlies (and rain) resulted in sea temperatures rising to 12.7°C—the warmest of the year (equaled 3 weeks later).

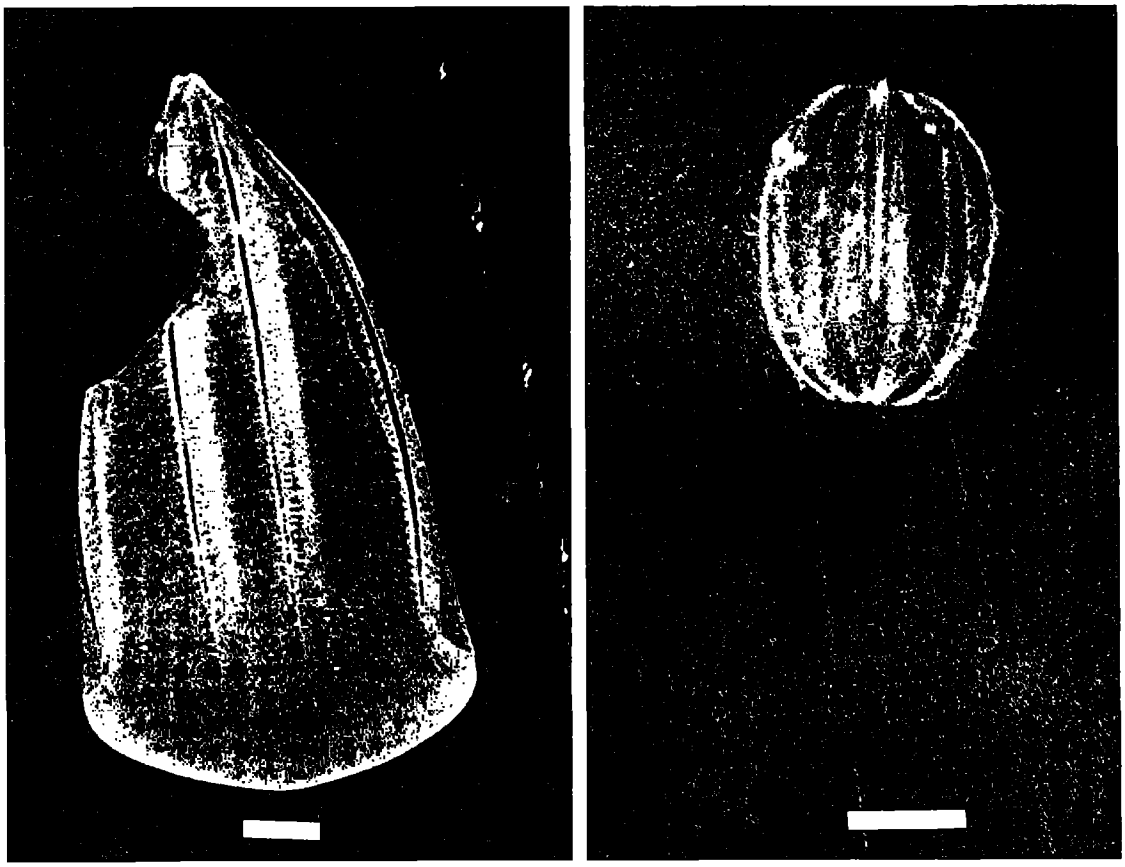


FIGURE 10.—Ctenophores off Mendocino. *Beroe forskali* (left), missing piece probably taken by planktivore, and *Pleurobrachia bachei* (right). Scale indicator = 1 cm.

EVENT 12—The process abruptly reversed with a shift to northerlies that gusted to 30 K for 2 days, and sea temperature fell to 11.5°C on 25 January.

EVENT 13—In another abrupt reversal, 3 days (27–29 January) of 15–25 K southerlies (with rain) resulted in sea temperature rising to 12°C.

EVENT 14—Reversing again, northerlies of 12–20 K on 30–31 January drove sea temperatures down to 10.5°C, at which point (1 February) the thermograph malfunctioned. Southerlies predominated while the thermograph was inoperative, and when it was reinstalled on 11 February, rising sea temperature 2 days later (13 February) equaled the season high of 12.5°C. But when northerlies returned the next day the downwelling season began its decline.

EVENT 15—Two days of 20–25 K northerlies (19–20 February) resulted in the season's largest 24-h change in sea temperatures.

EVENT 16—Sea temperature rose to 11.5°C on 3 March following 8 consecutive days of 8–15 K southerlies (with rain), or weak northerlies (to 6 K). An abrupt shift followed, as 2 days of 15–25 K northerlies (4–5 March) resulted in the season's second largest 24-h change in sea temperature—the first time since November that sea temperature had fallen below 10°C.

EVENT 17—After a week of light variable winds, during which sea temperatures remained essentially unchanged at about 9.8°C, southerlies increased to 15–20 K (on 15 March) and sea temperatures began rising to begin the final downwelling episode of the 1980–81 downwelling season (which was followed by the abrupt reversal that marked the beginning of the 1981 upwelling season, see Figure 4).

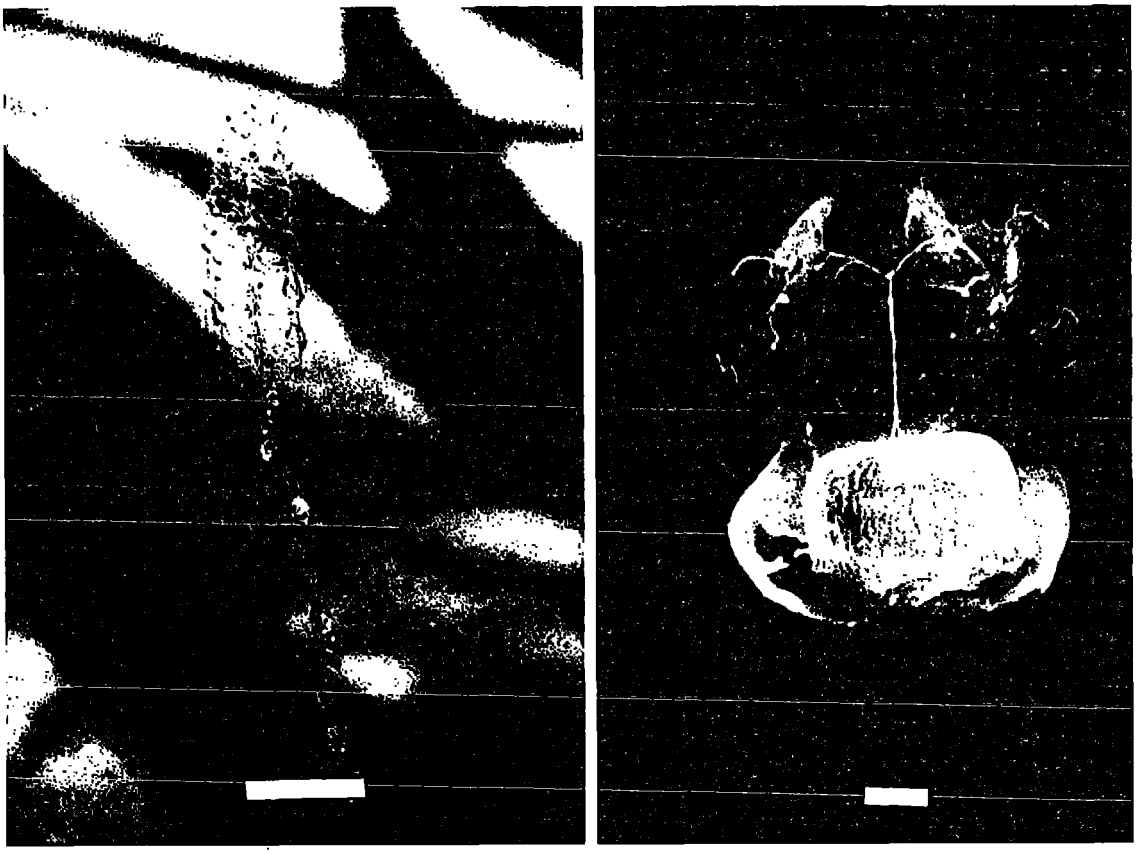


FIGURE 11.—Siphonophores off Mendocino. The physonect *Stephanomia bijuga* (left), and the calycophore *Praya dubia* (right). Scale indicator = 1 cm.

tions, but because fall and winter were so different, we consider them separately. We did not observe upwelling conditions during this period.

The major foods during six days of fall downwelling, based on the ranking indices (Table 4), were pelagic hydrozoans, specifically siphonophores, but vegetation comprised a larger part of the total diet volume. Virtually all plant materials taken at these times, however, were sori of *N. leutkeana*. As was true during the upwelling season, there tended to be more vegetation in the diet when there were fewer of the larger gelatinous zooplankters in the water column. For example, during the sampling session of 18 October 1978 (Table 1), when the surface plankton-collections took 400 siphonophores and ctenophores, only 1 of the 9 fish collected had consumed plant material (one sorus of *N. leutkeana*). On the other hand, during the sampling session of 16 October 1979 (Table 1), when the surface plankton-collection took only 30 siphonophores and ctenophores, 10 of 13 fish collected had consumed vegetation ($\bar{x}$ diet volume = 80%, virtually all of it sori of *N. leutkeana*; number taken = 1–21, $\bar{x}$ = 9.0), and two others were empty.

Our assessment of the diet and concurrent composition of the plankton during winter downwelling is limited to four days of sampling (Table 5). Data from these collections are combined for consistency

FIGURE 12.—Pelagic gastropods off Mendocino. The heteropod *Caranaria japonica* (upper), and the pteropod *Corolla spectabilis* (lower). Scale indicator = 1 cm. Often in areas where blue rockfish are feeding many of the *C. spectabilis* present have lost the bulbous central part of their body (pseudoconch and viscera).

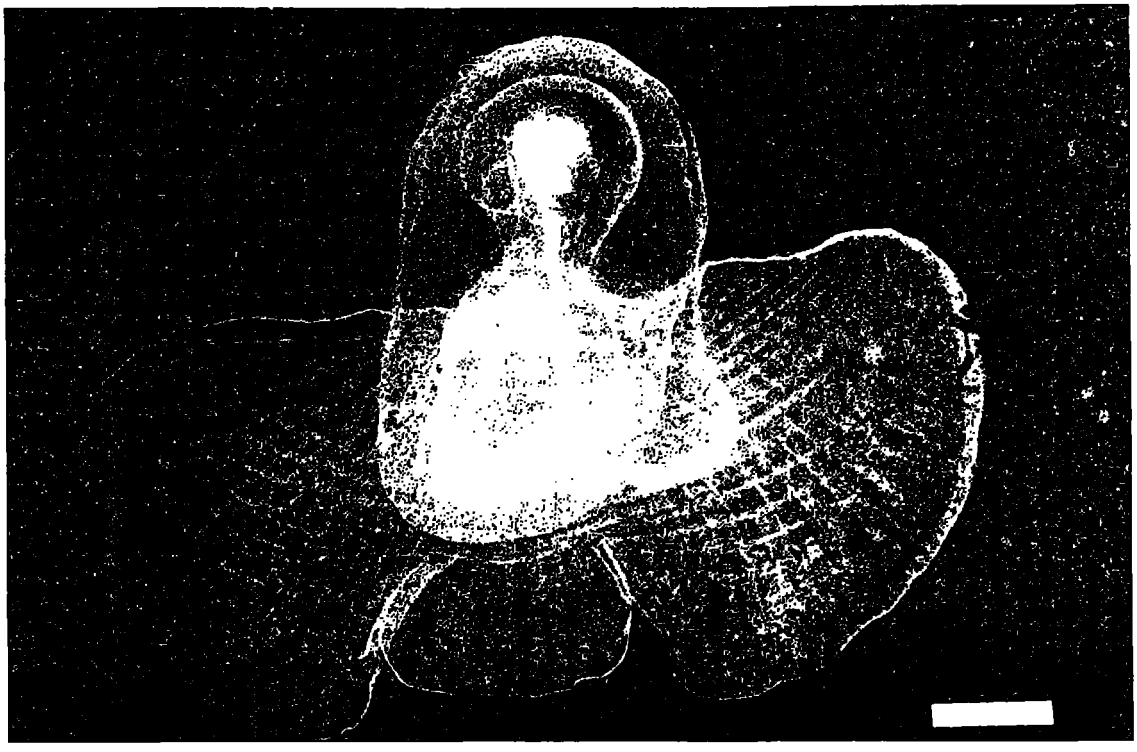


TABLE 4.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of fall. n = 6.

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	In diet: % occur.	In diet: $\bar{x}$ no.	In diet: $\bar{x}$ % vol.	In plankton: Size (mm)	In plankton: % occur.	In plankton: $\bar{x}$ no.[1]	In plankton: $\bar{x}$ % vol.
1	**PELAGIC HYDROZOA (10455.98)**	**2–15**	**46**	**18.04**	**12.5**	**1–25**	**83**	**1747.12**	**26.5**
	Hydromedusae								
	Eutonina indicans	18	1	0.03	<0.1	18–25	33	1516.81	14.7
	Others	15	4	0.02	<0.1	<1–20	33	26.10	0.2
	Syphonophora								
	Muggiaea atlantica	6–15	10	0.34	0.7	5–12	67	15.83	2.0
	Stephanomia bijuga	10	17	1.33	0.8	10	17	2.39	0.3
	Others	2–15	31	16.32	10.9	1–8	4	185.99	9.3
	Chondrophora								
	Velella velella[2]	—	0	0.00	0.0	NA[2]	NA	NA	NR
2	**PLANTS (4123.00)**	**NR[3]**	**54**	**2.06**	**37.1**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	51	1.94	35.6	NR	NR	NR	NR
	Porphyra sp.	NR	2	NR	0.2	NR	NR	NR	NR
	Smithora naidum	NR	6	0.06	<0.1	NR	NR	NR	NR
	Others	NR	6	0.06	1.3	NR	NR	NR	NR
3	**CTENOPHORA (1742.66)**	**3–15**	**33**	**5.74**	**9.2**	**<1–10**	**0.67**	**295.79**	**5.4**
	Pleurobrachia bachei	3–15	31	5.73	9.2	<1–10	50	288.59	5.2
	Others	12	1	0.01	<0.1	3	17	7.20	0.2
4	**PELAGIC GASTROPODA (554.00)**	**2–160**	**25**	**3.20**	**6.8**	**<1–45**	**100**	**187.82**	**8.4**
	Heteropoda								
	Caranaria japonica	12–160	15	0.33	2.1	30–45	17	1.21	0.7
	Pteropoda								
	Corolla spectabilis	5–22	16	2.69	4.7	2–20	50	72.90	7.5
	Limacina helicina	2	1	0.18	<0.1	1–3	17	109.80	0.2
	Others	—	0	0.00	0.0	<1–3	17	3.91	<0.1
5	**SCYPHOZOA (89.96)**	**10–35**	**18**	**0.51**	**9.8**	**NA**	**NA**	**NA**	**NA**
	Fragments	10–35	18	0.51	9.8	NA	NA	NA	NA
6	**THALIACEA (31.97)**	**5–29**	**16**	**0.54**	**3.7**	**2–5**	**17**	**3.01**	**NR**
	Undetermined species	5–29	16	0.54	3.7	2–5	17	3.01	NR
7	**EUPHAUSIACEA (22.93)**	**4–10**	**21**	**0.78**	**1.4**	**<1–9**	**67**	**162.90**	**2.2**
	Larvae	4	1	0.01	<0.1	4	50	129.01	1.2
	Thysanoessa spp.	4–10	19	0.74	1.4	5–9	33	33.89	1.0
	Others	8	1	0.03	<0.1	—	0	0.00	0.0

with the other tables and figures, but the combinations obscure the great variation in feeding conditions at this time of year. For example, taxa of the major food categories listed in Table 5 were numerous in the diet and plankton only during the two sampling sessions in February and March of 1979. Of the 14 fish collected at those times, all but one was well fed ($\bar{x}$ no. prey = 26.7), with the exception being a pregnant female whose gut was empty. Thaliaceans dominated on these occasions, both in the diet and in the plankton, and hyperiid amphipods, *Vibilia* spp. (which are parasites of thaliaceans (Laval 1980)), were similarly abundant. In contrast, the collecting session of January 1980 indicated there were more zooplankters in the water column, but that they were exceptionally small. The plankton collection took 1,488 zooplankters (compared with 109 and 715 in the two 1979 collections), but only 2% were of species that occurred as large as 2 mm (compared with 86% in 1979). That these small zooplankters were unsuitable as prey of adult *S. mystinus* is implicit in the fact that of 16 fish collected, only 3 contained food—all of it the alga *Porphyra* sp. (The other 13 represented 76% of all fish with empty guts in the winter collections.) Significantly, of the taxa identified as food of adult *S. mystinus* during the winter (Table 5), only one, the calanoid *Calanus pacificus*, was represented in the January 1980 plankton collection. Conditions were intermediate during the sampling session of January 1981, when some of the listed food taxa occurred in both diet and plankton (though in reduced numbers) and five of eight fish sampled contained food.

TABLE 4.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	% occur.	$\bar{x}$ no.	$\bar{x}$ % vol.	In plankton: Size (mm)	% occur.	$\bar{x}$ no.[1]	$\bar{x}$ % vol.
8	**CALANOIDA (14.32)**	**2–7**	**22**	**0.93**	**0.7**	**<1–7**	**100**	**9528.11**	**28.3**
	Nauplii	—	0	0.00	0.0	<1–1	33	68.99	<0.1
	Acartia spp.	—	0	0.00	0.0	<1–1	83	1751.42	4.3
	Calanus pacificus	3	6	0.13	<0.1	<1–4	83	4609.21	15.8
	Eucalanus californicus	4–7	15	0.67	0.7	2–7	100	255.39	1.2
	Rhincalanus nasutus	4	4	0.06	<0.1	—	0	0.00	0.0
	Others[4]	2–3	3	0.07	<0.1	<1–3	100	2843.10	7.0
9	**HYPERIIDEA (8.28)**	**1–8**	**24**	**1.15**	**0.4**	**1–7**	**83**	**292.19**	**0.4**
	Hyperoche medusarum	2	3	0.16	0.1	1–7	50	273.01	0.2
	Vibilia spp.	—	0	0.00	0.0	—	0	0.00	0.0
	Others	1–8	21	0.99	0.3	1–3	33	19.18	0.2
10	**POLYCHAETA (3.20)**	**4–40**	**16**	**0.40**	**0.5**	<1–7	83	118.21	1.7
	Larvae	—	0	0.00	0.0	<1–4	33	103.81	1.5
	Postlarvae	4–40	16	0.40	0.5	3–7	50	14.40	0.2
	OTHER CATEGORIES								
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	189.59	0.7
	Cladocera	—	0	0.00	0.0	<1–1	33	142.20	0.8
	Cyclopoida	NR	1	0.01	NR	<1–1	67	648.00	4.0
	Cirripedean larvae	—	0	0.00	0.0	<<1–<1	67	128.70	0.2
	Reptantian larvae	—	0	0.00	0.0	<1–6	83	52.20	0.3
	Natantian larvae	—	0	0.00	0.0	1–5	33	237.60	NR
	Bryozoan larvae	—	0	0.00	0.0	<1	33	244.49	0.2
	Larvacea	2	3	0.12	0.1	<1–4	67	844.20	2.8
	Chaetognatha	10–11	3	0.06	0.2	5–20	83	225.59	5.0
	Eggs, undetermined	—	0	0.00	0.0	<1	17	1535.99	4.3
	Eggs, fish	3	1	0.01	<0.1	<1–2	33	40.19	4.4
	Fishes	6–24	4	0.04	0.2	4–20	33	5.40	0.7
	UNIDENTIFIABLE MATERIAL[5]	—	—	—	17.4	—	—	—	—
	No. fish examined: 73 218–350, $\bar{x}$ = 290.3 mm SL No. empty = 7 $\bar{x}$ no. prey: individuals = 32.4 taxa = 3.6					No. plankton collections: 6 $\bar{x}$ no. zooplankters: 9663.0			

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]Many of the calanoids from the plankton included in this category were juveniles and other undetermined stages of the species distinguished above. Most were at the lower end of the size range indicated.
[5]Digested beyond recognition.

DISCUSSION

It is clear that wind-driven movement of the surface water profoundly influences feeding by *Sebastes mystinus* off northern California. Water set in motion by the wind can be tens of meters deep (Bakun 1973; Barber and Smith 1981), and so carries most of the foods of nearshore planktivores. The movement is seaward (with upwelling) under northerly winds and shoreward (with downwelling) under southerly winds. Thus, with winds along the Mendocino coast being northerly or southerly about 80% of the time (based on records of the NOAA weather station there), adult *S. mystinus* in that area alternate between periods when planktonic foods are being carried into their habitat and periods when these foods are being carried away.

This perception of alternations between upwelling and downwelling is simplified, perhaps overly so, to emphasize features we consider essential to the feeding of *S. mystinus*, and also because details of what clearly is a complex oceanographic system remain unclear. In particular, we stress the importance of shoreward surface transport in carrying prey to *S. mystinus* in nearshore habitats. The major prey of adult *S. mystinus*—thaliaceans, pelagic hydrozoans, and other relatively large, gelatinous zooplankters—tend to be concentrated in areas of oceanic convergence, and dispersed in areas of oceanic divergence (e.g., Bakun and Parrish 1980). Thus, when offshore surface waters converge on the coast, the planktonic foods of *S. mystinus* become concentrated near shore.

TABLE 5.—Food of adult *Sebastes mystinus* relative to near-surface plankton during downwelling episodes of winter. n = 4.

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	In diet: % occur.	In diet: $\bar{x}$ no.	In diet: $\bar{x}$ % vol.	In plankton: Size (mm)	In plankton: % occur.	In plankton: $\bar{x}$ no.[1]	In plankton: $\bar{x}$ % vol.
1	THALIACEA (29034.03)	**7–20**	**71**	**12.90**	**31.7**	**5–45**	**50**	**9.90**	**34.8**
	Undetermined species	7–20	71	12.90	31.7	5–45	50	9.90	34.8
2	HYPERIIDEA (3278.81)	**1–5**	**62**	**23.40**	**2.2**	**1–6**	**75**	**2.25**	**0.8**
	Hyperoche medusarum	—	0	0.00	0.0	4	25	0.45	NR[3]
	Vibilia spp.	1–5	57	23.06	2.1	5–6	25	0.90	0.8
	Others	6	5	0.34	0.1	1	25	0.90	NR
3	EUPHAUSIACEA (1567.61)	**6–12**	**43**	**11.76**	**3.1**	**10**	**75**	**2.25**	**12.5**
	Larvae	—	0	0.00	0.0	—	0	0.00	0.0
	Thysanoessa spp.	6–12	38	11.67	3.1	10	75	2.25	12.5
	Others	6	5	0.09	<0.1	—	0	0.00	0.0
4	SCYPHOZOA (1054.20)	**NR**	**38**	**1.43**	**19.4**	**NR**	**NR**	**NR**	**NR**
	Fragments[2]	NR	38	1.43	19.4	NR	NR	NR	NR
5	PELAGIC GASTROPODA (726.34)	**6–30**	**48**	**2.91**	**5.2**	**1–20**	**25**	**8.10**	**0.8**
	Heteropoda								
	Caranaria japonica	15–30	10	0.24	0.5	—	0	0.00	0.0
	Pteropoda								
	Corolla spectabilis	6–20	48	2.67	4.7	20	25	0.45	0.8
	Limacina helicina	—	0	0.00	0.0	1–2	25	7.65	NR
	Others	—	0	0.00	0.0	—	0	0.00	0.0
6	PELAGIC HYDROZOA (437.91)	**3–13**	**43**	**1.52**	**6.7**	**1–6**	**75**	**14.85**	**1.3**
	Hydromedusae								
	Eutonina indicans	—	0	0.00	0.0	—	0	0.00	0.0
	Others	10–22	40	0.33	3.5	1–4	50	12.60	0.5
	Syphonophora								
	Muggiaea atlantica	8–13	38	0.86	2.1	6	50	1.35	0.8
	Stephanomia bijuga	—	0	0.00	0.0	—	0	0.00	0.0
	Others	3–20	19	0.33	1.1	3	25	0.90	NR
	Chondrophora								
	Velella velella	—	0	0.00	0.0	NA[4]	NA	NA	NA
7	PLANTS (380.00)	**NR**	**38**	**NR**	**10.0**	**NR**	**NR**	**NR**	**NR**
	Nereocystis sori	NR	5	0.10	0.1	NR	NR	NR	NR
	Porphyra sp.	NR	19	NR	5.2	NR	NR	NR	NR
	Smithora naidum	—	0	0.00	0.0	NR	NR	NR	NR
	Others	NR	19	NR	4.7	NR	NR	NR	NR

Shoreward transport can be either wind-driven (Ekman transport), or result simply from relaxation of the forces that drive upwelling. But in either case our observations indicate that shoreward flowing surface waters override the colder waters near shore, a process we refer to as downwelling. Usually the term downwelling is limited to conditions that result from shoreward Ekman transport (e.g., Gross 1977), but we have found that relaxation of upwelling has essentially the same effect on the nearshore ecosystem, the difference being simply in degree of effect.

Some studies have concluded that warming of the nearshore surface waters during relaxation of upwelling results from alongshore advection (e.g., Send et al. 1987), but even though zooplankters entering our study area during downwelling generally moved southward along the coast, the characteristic presence of such forms as thaliaceans, ctenophores, and pteropods indicate that the advection is from offshore. So despite the complexities of circulation and mixing that occur in the coastal waters off northern California (e.g., Winant et al. 1987), the net result affecting the trophic relations of *S. mystinus* are alternations between seaward and shoreward transport.

These water movements follow a strong seasonal pattern that is evident in upwelling indices for lat. 39°N (which crosses Mendocino) produced by the Pacific Fisheries Environmental Group of the Southwest Fisheries Center, NMFS, NOAA. In addition to the seasonal trend, short-term episodes of seaward and shoreward transport produce day-to-day, even hour-to-hour, changes in the foods available to

TABLE 5.—*Continued.*

Rank	Food organism: Taxa (rank index)	In diet: Size (mm)	In diet: % occur.	In diet: $\bar{x}$ no.	In diet: $\bar{x}$ % vol.	In plankton: Size (mm)	In plankton: % occur.	In plankton: $\bar{x}$ no.[1]	In plankton: $\bar{x}$ % vol.
8	CTENOPHORA (4.73)	**11–20**	**10**	**0.43**	**1.1**	—	**0**	**0.00**	**0.0**
	Pleurobrachia bachei	11	5	0.09	0.1	—	0	0.00	0.0
	Others	20	5	0.34	1.0	—	0	0.00	0.0
9	MYSIDACEA (4.47)	**6–20**	**14**	**0.29**	**1.2**	**3–8**	**50**	**1.80**	**0.5**
	Acanthomysis sculpta	6	5	0.19	1.0	—	0	0.00	0.0
	Others	18–20	10	0.10	0.2	3–8	50	1.80	0.5
10	CALANOIDA (1.18)	**2–5**	**14**	**0.28**	**0.3**	**1–5**	**100**	**684.00**	**25.6**
	Nauplii	—	0	0.00	0.0	—	0	0.00	0.0
	Acartia spp.	—	0	0.00	0.0	<1–1	25	229.50	7.5
	Calanus pacificus	2–3	14	0.14	0.1	1–3	100	110.70	3.8
	Eucalanus californicus	5	10	0.14	0.2	3–5	50	12.60	0.8
	Rhincalanus nasutus	—	0	0.00	0.0	—	0	0.00	0.0
	Others	—	0	0.00	0.0	1–2	100	331.20	13.5
OTHER CATEGORIES									
	Molluscan larvae	—	0	0.00	0.0	<<1–<1	50	38.70	2.5
	Cyclopoida	—	0	0.00	0.0	1	75	61.20	1.5
	Cirripedean larvae	—	0	0.00	0.0	1–2	75	24.75	0.5
	Reptantian larvae	4	<1	0.05	<0.1	<1–3	100	240.30	9.3
	Larvacea	—	0	0.00	0.0	3–6	50	6.30	1.3
	Chaetognatha	—	0	0.00	0.0	5–35	75	14.85	5.0
	Fishes	8–10	<1	0.10	NR	3–7	75	7.65	2.8
UNIDENTIFIABLE MATERIAL[5]		—	—	—	19.1	—	—	—	—

No. fish examined: 38
200–345, $\bar{x}$ = 265.3 mm SL
No. empty: 17
$\bar{x}$ no. prey: individuals = 45.2
taxa = 4.8

No. plankton collections: 4
$\bar{x}$ no. zooplankters: 634.3

[1]Value is estimated mean number per 100 m³ of water, based on water filtered (54.8 m³) during the 5-min collection.
[2]Adult *S. mystinus* often were seen feeding on large individuals of *Cyanea capillata*, which were avoided by us during plankton collections because they would have made collections unmanageable.
[3]NR = not recorded. The enumeration was either omitted or unfeasible.
[4]*Velella velella* floats on the water's surface, where it was not effectively sampled by our net.
[5]Digested beyond recognition.

planktivorous fishes. The following discussion considers how the diet of *S. mystinus*, summarized in Figure 13, is influenced by these alternations in surface transport during distinct upwelling and downwelling seasons.

The Upwelling Season

The spring-summer upwelling season produces optimal feeding conditions for *S. mystinus*. During this period the combined effects of increased nutrients (from strong upwelling) and increased daylight (from longer days, higher sun-angle, and less storm-produced sediments in suspension) result in growth of diatom populations that constitute the food-base of the zooplankton community.

Seaward Ekman transport in response to the season's persistent northerly winds carries the upwelled nutrients and increasing number of diatoms offshore, where the response of zooplankters can be spectacular. Consider, for example, thaliaceans, which are a major prey of adult *S. mystinus*. Recent study has shown that populations of *Salpa fusiformis* (a common thaliacean in the California Current) normally are food-limited, but can grow rapidly when diatoms are abundant (Silver 1975). In response to a diatom bloom, *Thalia democratica* (another salp common in the California Current), can increase in size by up to 10%/hour and in numbers up to 2.5 times/day, the highest rate recorded for a metazoan animal (Heron 1972a, b).

Zooplankters thus increased in size and number are then carried to *S. mystinus* near shore by the shoreward flow that develops with relaxation of upwelling, or, more forcefully, with shoreward Ekman transport under southerly winds. It remains uncertain, however, whether the numbers of zooplankters entering the Mendocino nearshore habitats are in fact related to the productivity of local upwelling. Wickett (1967) concluded that zooplankton abun-

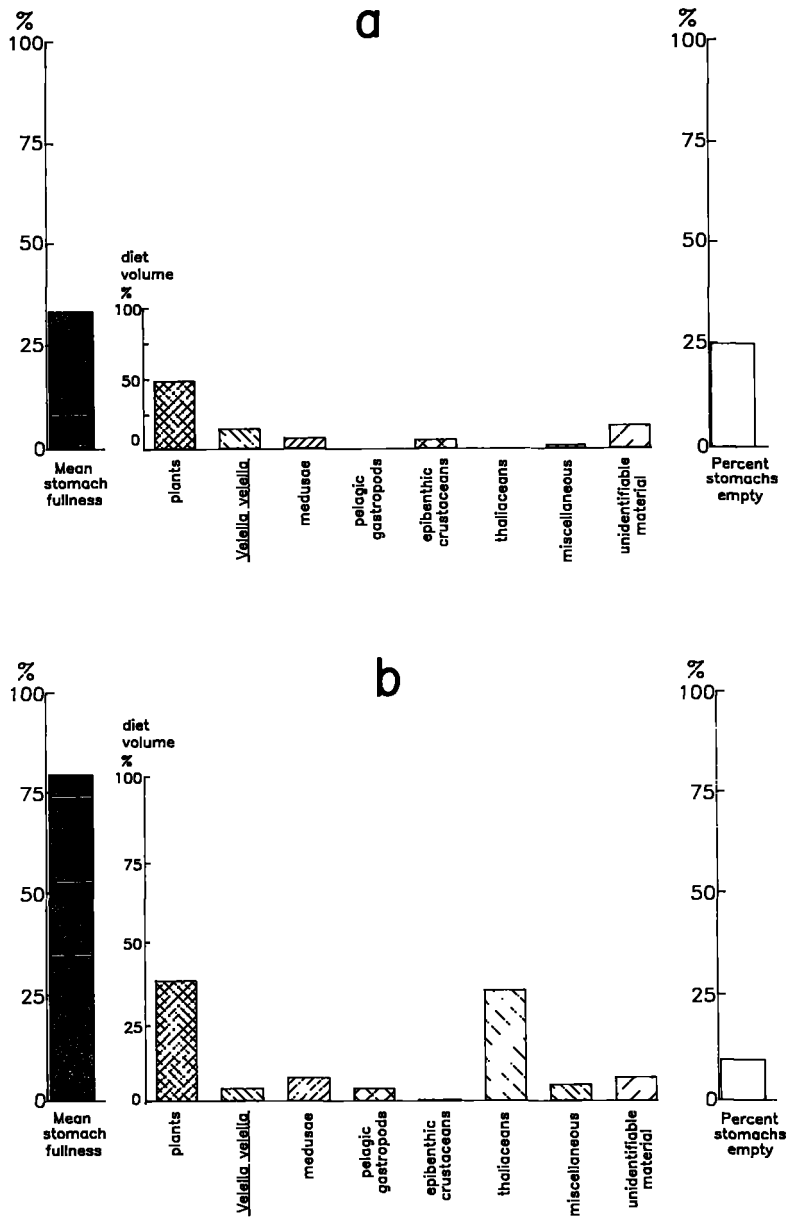
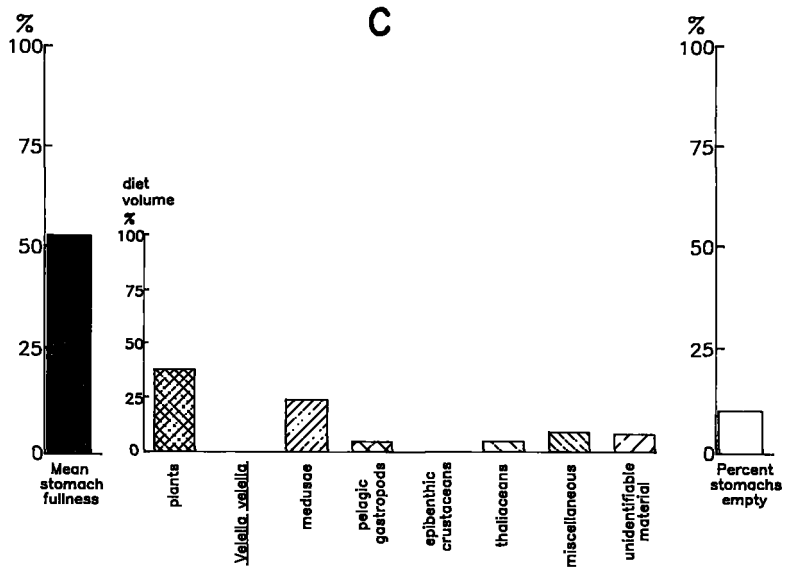


FIGURE 13.—Seasonal variations in the diet of *Sebastes mystinus*:
a. Diet during upwelling episodes of the upwelling season. $n = 51$.
b. Diet during downwelling episodes of the upwelling season. $n = 85$.



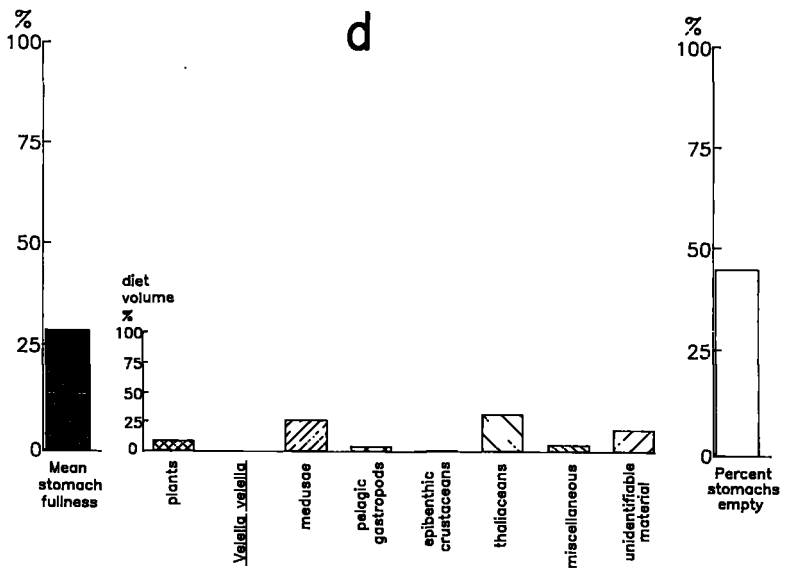


FIGURE 13.—*Continued*—Seasonal variations in the diet of *Sebastes mystinus*:

c. Diet during fall of the downwelling season. n = 73.

d. Diet during winter of the downwelling season. n = 38.

dances off California depend on nutrients from the Gulf of Alaska, and Chelton et al. (1982) concluded not only that phytoplankton off California depend on nutrients from higher latitudes but also that wind-forced coastal upwelling is relatively unimportant in supplying these nutrients. Despite this uncertainty, growth in thaliaceans is so rapid that it would seem at least many of those off the Mendocino coast could result from local upwelling. Regardless of what determines the growth of thaliaceans in this region, their appearance in large numbers next to the beach is evidence that shoreward transport has developed. These animals are readily detected by in situ observations, and also by their occurrences in samples of both plankton and gut contents (Table 3).

Intermittent shoreward transport during the upwelling season seems especially strong off northern California. This is evident in the upwelling indices of Bakun (1973), and also in that fewer thaliaceans get inshore at this time of year, both to the north, off Oregon (Hubbard and Pearcy 1971), and to the south, off central and southern California (Blackburn 1975). Thus, it is clear that the major foods of *S. mystinus* along the Mendocino coast are most available during downwelling episodes of the upwelling season.

Despite the increased productivity of the upwelling season, *S. mystinus* experiences relatively poor feeding conditions during that season's upwelling episodes. Not only are fewer prey taken during upwelling than during downwelling, a higher proportion of the fish have empty stomachs (Fig. 13). This is because the shoreward flow that transports zooplankters from offshore during downwelling is replaced by the seaward flow that is part of the upwelling condition.

There is, however, one relatively large gelatinous zooplankter from offshore that is most available as prey during upwelling. This is the chondrophore *Velella velella*, a pelagic hydrozoan known as "by-the-wind-sailor". It is, in fact, entirely because of this animal that the food category "Pelagic Hydrozoa" ranked second as food during upwelling episodes (Table 2). Because *V. velella* floats on the water's surface and is equipped with a sail-like structure (Fig. 8), its movements are determined more by wind than by current. The species includes two forms distinguished by whether their sails are oriented to the left of or to the right of the main body axis. This orientation determines their direction in sailing before the wind—left-handed individuals sail to the left of the wind direction and right-handed individuals sail to the right (Bieri 1959). Although it has been reported that the right-handed form predominates off California (Morris et al. 1980), all those we examined from off Mendocino were left-handed, and so would have been driven shoreward by the northerly winds that generated upwelling.

In the absence of favored open-water zooplankters, *S. mystinus* increased consumption of nearshore hyperbenthic zooplankton, e.g., mysidaceans and gammarideans (Table 2). But fewer of these organisms were taken than might be expected, based on their great abundance during much of the upwelling season. *Acanthomysis sculpta*, the mysid most often taken as prey, typically aggregates in large swarms within 2 m of the seafloor. To prey on them, adult *S. mystinus* must leave the upper levels of the water column in a departure from their usual feeding mode that may reduce feeding effectiveness. In addition, most hyperbenthic zooplankters probably are too small to be ready prey of these fish. Although 5–7 mm mysids (Table 2) should be large enough, most other taxa are less than 2 mm. Organisms as small as 1 mm occur in the diet, including some thought to be strictly benthonic, e.g., smaller of the gammaridean *Jassa* sp. (which also occurred in plankton collections; Table 2). But such forms may be ingested (and taken by plankton nets) while attached to drifting plant fragments. Although *S. mystinus* has a smaller mouth than most of its congeners, presumably as an adaptation to planktivory (Hallacher and Roberts 1985), the adults appear unable to consume the larvae of neritic species, e.g., cirripedeans, that, with maximum dimensions of 1 mm or less, often are the most numerous of the zooplankton (Table 2). These larvae are major prey of juvenile *S. mystinus* (unpubl. data; Gaines and Roughgarden 1987), which further suggests it is their small size that precludes them as prey of the adult.

Foods most often consumed in the absence of preferred zooplankters, however, were plant materials. In fact, during upwelling episodes more plants were consumed than anything else (Table 2), and even during downwelling plants were the second-ranked food category (Table 3). Although these rankings are inflated by undigested plant tissues, certain algal materials appear to be important foods. The availability of plant foods to supplement prey shortages was strongly seasonal, however. Thus, the sharply reduced availability of plants during winter and early spring undoubtedly contributed to the prevalence of empty stomachs among fish collected at those times.

Although a wide variety of plants were ingested, *S. mystinus* seemed able to utilize only certain algal tissues. These included zoospores of *Nereocystis leutkeana* and the two epiphytes, *Porphyra nereocystis* and *Smithora naidum*. Probably this is because as members of a carnivorous family they have only limited abilities to digest plant material.

The zoospores of *N. leutkeana* are especially vulnerable to *S. mystinus* when the sori have dropped from the plants' fronds, because at this time the sori have lost their epidermis (an adaptation of the mature sori that facilitates release of the zoospores (David C. Walker[2]). Zoospores may be appropriate food for this largely carnivorous fish because they are, as their name implies, animal-like: they have cell membranes but not the cellulosic cell walls (Wilson 1952) that preclude plants as food for many fishes (e.g., Lobel 1981). The other algae apparently utilized—*Porphyra nereocystis* and *Smithora naidum*—may be appropriate forage for a fish with limited herbivorous abilities because they are monostromatic plants only 25–60 μ thick (Abbott and Hollenberg 1976). So while Gotshall et al. (1965) reported that algae in the guts of *S. mystinus* generally are undigested, some forms appear to be important foods.

It is possible that plant materials are among items of little or no food value that are ingested during food shortages simply because at such times the adult *S. mystinus* become less discriminating in their choice of drifting objects. On the other hand, it is also possible that these fish have unusual herbivorous abilities as a result of adaptations to a diet rich in thaliaceans, which are among the few animals with cellulosic tissues (Berrill 1961). This second possibility is weakened, however, by the fact that the cellulosic tunics of the thaliaceans appear to pass through the gut undigested (Gotshall et al. 1965; our observations).

The Downwelling Season

As the downwelling season developed in the fall, *S. mystinus* experienced progressively poorer feeding conditions. Offshore water flowing into the nearshore habitats at these times tended to be poor in phytoplankton (hence its transparency and blueness, in contrast to the turbid greenness of a few months before), and so generally lacked the herbivorous thaliaceans that were major prey during periods of peak feeding. Relatively large gelatinous zooplankters continued on occasion to be numerous in the shoreward flow, but the species at this time tended to be carnivores rather than herbivores, and *S. mystinus* did not feed on some of them. For example, while siphonophores made "Pelagic Hydrozoa" the top-ranked food category (Table 4), the most numerous pelagic hydrozoan in the water column, *Eutonina indicans*, went virtually untaken. (The small medusae visible throughout Figure 1, especially against the dark kelp, are of this species.) On the other hand, another relatively large, gelatinous zooplankter, the ctenophore *Pleurobrachia bachei* (Fig. 10), was prominent both as prey and in the plankton. Probably the presence of *P. bachei* accounted for the gut-content occurrences of the hyperiid *Hyperoche medusarum*, which is a parasite of this ctenophore (Brusca 1970).

As was true during late spring and summer, certain plant materials became major foods during the fall when favored zooplankters were in short supply. But unlike late spring and summer, when many different plant forms were taken, virtually the only plant materials consumed in the fall were the sori of *N. leutkeana*. This reflected a decreasing abundance of other plants in the environment at the time. Nevertheless, while sporophytes of *N. leutkeana* were fewer in fall than in summer, those present were larger, more mature, and produced more sori.

Although winter produced the poorest feeding conditions of the year, with by far the highest incidence of empty stomachs among the fish examined (Figure 13; also noted by Gotshall et al. 1965), occasionally the waters flowing into the nearshore habitats were rich in offshore zooplankters, including thaliaceans, and at these times the fish fed well. Our sampling of the highly varied winter conditions was not frequent enough to recognize a pattern, but they differed from fall conditions. In general, the distinctive fall and winter conditions off Mendocino matched the "oceanic" and "Davidson Current" oceanographic seasons defined by Skogsberg (1936) and Bolin and Abbott (1962) for Monterey Bay.

Ekman Transport and the Distribution of *Sebastes mystinus*

Ekman transport may be important to the distribution of *S. mystinus*. This is implicit in our finding that alternations between seaward and shoreward surface transport produce feeding opportunities for

[2]David C. Walker, Department of Botany, University of British Columbia, Vancouver, British Columbia V6T 1W5, Canada, pers. commun. 10 May 1977.

which the species is particularly well adapted. Along the west coast of North America, these alternations are best developed off northern and central California (Bakun 1973; Bakun et al. 1974; Mason and Bakun 1985). And not only is *S. mystinus* most numerous off this same section of the coast, it is perhaps the dominant fish in the nearshore habitat there (Hallacher and Roberts 1985; Bodkin 1984; our observations). Although the species is reported from northern Baja California, Mexico, to the Bering Sea (Miller and Lea 1972), its numbers are sharply reduced northward from northern California (Alverson et al. 1964; Frey 1971; Hart 1973) and southward from central California (Hubbs 1948; Limbaugh 1955; Quast 1968). Although undoubtedly other factors are involved, we suggest that occurrences of *S. mystinus* in these northern and southern regions are limited by less favorable feeding conditions.

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Daniel Howard assisted in the field work and performed various aspects of data processing. Michael Bowers prepared the histological sections represented by Figure 7, and Louis Rouleau, NOAA weather observer at Mendocino, provided wind data used in Figures 4 and 9. For constructive criticism of the manuscript we thank Andrew Bakun, John Hunter, William Pearcy, and Richard Rosenblatt. Rahel Fischer typed the manuscript.

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THE REPRODUCTIVE BIOLOGY OF TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS* GOODE AND BEAN, FROM THE UNITED STATES MID-ATLANTIC BIGHT, AND THE EFFECTS OF FISHING ON THE BREEDING SYSTEM

CHURCHILL B. GRIMES,[1] CHARLES F. IDELBERGER,[2] KENNETH W. ABLE,[3] AND STEPHEN C. TURNER[4]

ABSTRACT

To investigate the reproductive biology of tilefish, *Lopholatilus chamaeleonticeps* Goode and Bean, we sampled the commercial longline fishery from 1978 to 1982. Results suggested that tilefish are fractional spawners from March to November with a spawning peak from May to September. Estimates of fecundity ranged from about 195×10^3 to 10×10^6 (for 53 cm FL, 2.1 kg and 91 cm FL, 13 kg females), but only 60–85% of the ovarian eggs appeared to have been released by the end of the spawning season.

Tilefish are apparently gonochoristic however, some adult males had slight amounts of ovarian tissue within the testicular mass. Sex ratios were skewed in favor of males at larger sizes; however, both sexes were present at most ages. All juveniles and unsexed fish (<400 mm FL) appeared to be female (i.e., gonad cell structure consisted of oogonia and previtellogenic oocytes), suggesting that some tilefish may undergo prematurational sex reversal, or that early gonad development involves an all female appearing stage.

Tilefish may have a complex breeding system that is behaviorally mediated. Both sexes are functionally mature at ca. 50 cm FL and 5 years, but some males appear to delay participation in spawning for 2–3 years and 10–15 cm in additional length. Tilefish are sexually dimorphic, with males attaining larger sizes and developing conspicuously enlarged predordal adipose flaps (an apparent indicator of male breeding status) at 65–70 cm FL (6–7 years), when males begin to participate in spawning (i.e., develop large testes), not when they are functionally mature (i.e., producing sperm).

The rapidly expanding fishery from 1978 to 1982, which reduced population density by one-half to two-thirds, may have altered the breeding system by causing males to spawn at smaller sizes (10 cm) and younger ages (2–2.5 years) in 1982 than in 1978.

Tilefish, *Lopholatilus chamaeleonticeps* (Branchiostegidae), is a demersal gonochoristic species found along the outer continental shelf from Nova Scotia south to Surinam (Dooley 1978; Markle et al. 1980). Within the Mid-Atlantic Bight (continental shelf between Cape Cod, MA and Cape Hatteras, NC), they inhabit a narrow zone of relatively warm temperatures (9°–14°C) in about 80–240 m depths. Following a brief period as pelagic larvae (Fahay and Berrien 1981; Berrien 1982), juveniles settle to the bottom. Adults are sexually dimorphic, males having larger adipose flaps (= predorsal crest of Dooley 1978) than females (Katz et al. 1983). Growth in both sexes is about 10 cm per year for the first four years, then it slows, but more so in females than males (Turner et al. 1983). Maximum size of females is about 100 cm FL and 112 cm FL in males, and maximum ages are 35 and 26 years, respectively (Turner et al. 1983).

Both juveniles and adults select sedimentary substrata, and seek shelter in a variety of habitats. Grossman et al. (1985) found a strong correlation between sediment composition and tilefish occurrence. Juveniles and adults occupy highly contageously distributed vertical burrows, the primary habitat, in Pleistocene clay substrata (Able et al. 1982; Grimes et al. 1986). Adults also inhabit horizontal excavations in more vertically oriented clay sediments of submarine canyon walls called "pueblo habitats" (Cooper and Uzmann 1977; Warme et al. 1977; Grimes et al. 1986), and scour depressions under and around glacial erratic boulders (Valen-

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tine et al. 1980; Grimes et al. 1986). Several crustaceans and fishes are concentrated in and near tilefish excavations, which are formed by the combined activity of tilefish and their associates (Able et al. 1982; Grimes et al. 1986). Several associates are important components of tilefish diets, suggesting close trophic linkages within the burrow community (Turner and Freeman MS[5]; Grimes et al. 1986). Limited mark-recapture data suggests that tilefish are sedentary (Grimes et al. 1983). Tilefish and their associates have definite temporal activity patterns, and male-female pairing may occur (Grimes et al. 1986). Habitat preference, contagious distribution within suitable clay substratum, definitive activity patterns, limited movement, and pair bonding provide opportunities for social interaction and organization within populations.

Commercial landings of the Mid-Atlantic–southern New England tilefish stock (Katz et al. 1983) have varied widely since 1916 when 4,500 metric tons (t) were landed in 10 months (Freeman and Turner 1977). In the early 1970s an important longline fishery developed, centered in New York-New Jersey, and landings increased. This fishery became one of the most valuable finfisheries in both states during most years since 1978 (Grimes et al. 1980; U.S. Department of Commerce 1980a–c; D. J. Christensen pers. commun.[6]). From 1977 to 1980, annual landings were 2,061, 3,412, 3,840, and 3,575 t, but catches declined to 3,200 and 1,900 t in 1981 and 1982 (U.S. Department of Commerce 1980a–c; D. J. Christensen fn. 6). Effects of fishing on the stock have been drastic, reducing stock size by one-half to two-thirds from 1978 to 1982 (Turner 1986).

The purpose of this paper is to describe the reproductive biology of tilefish in the northern stock, and present evidence that participation in spawning by males is socially mediated. Furthermore, we show that the mating system has been modified by commercial fishing.

MATERIALS AND METHODS

Samples of tilefish from the United States Mid-Atlantic–southern New England area were obtained from domestic longline and New Jersey recreational (headboat[7]) fisheries. Information gathered for each sample included the statistical nature of the sample (random or nonrandom), capture method, location (LORAN C), date, and length (FL, cm), sex, weight (whole and eviscerated), and height (mm) of the adipose flap of each animal. When possible, gonads were excised, weighed (0.1 g) and preserved in 10% formalin. We assigned each fish to one of three classifications (male, female, or unknown) and one of six stages of sexual maturity following visual examination (Nikolsky 1963). Some fish used for reproductive studies were aged using thin sections of their saggital otoliths (Turner et al. 1983).

Routine histological sectioning and staining (haemotoxylin and eosin) techniques and light microscropy (450× and 1000×) were used to examine gonad structure of six small fish (<50 cm), and assess the state of sexual maturity. Ovarian development corresponded to that described by Moe (1969) for red grouper, *Epinephelus morio*, and Yamamoto (1956) for the flounder *Liopsetta obscura*. Spermatogenic development was identical to that of *Tilapia leucosticta* (Hyder 1969) and toadfish, *Opsanus tau*, (Hoffman 1963). Females were assessed as immature when ovaries contained only previtellogenic and early vitellogenic oocytes (Yamamoto 1956; Moe 1969; Waltz et al. 1982; Ross 1978; Erickson and Grossman 1986). Males were considered mature when active spermatogenesis was occurring and spermatozoa were present in spermatogenic tubules (Ross 1978). Limited spermatogenesis occurred in the testes of some immature males (Erickson and Grossman 1986).

A gonosomatic index (GSI) was calculated for females according to the formula $GSI = \frac{GW}{BW} \times 100$, where GW = fresh gonad weight (g) and BW = fresh eviscerated body weight (g) (Nikolsky 1963), for describing spawning seasonality. The seasonal progression of mean ovum diameters was also used to establish the reproductive seasonality, and the ovum-diameter frequency distribution for ripe females was used to indicate spawning frequency (isochronal vs. heterochronal) (Hickling and Rutenberg 1936). Separated ova from each fish were placed in liquid and stirred; a random sample for measuring was then obtained by extracting three aliquots with a large syringe. Diameters of 500–1,000 ova from each female were measured (nearest ocular micrometer unit) using a binocular dissecting scope and a filar micrometer. We assumed

[5]Turner, S. C., and B. L. Freeman. Food habits of tilefish, *Lopholatilus chamaeleonticeps*. Unpubl. manuscr. Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Miami, FL 07732.

[6]D. J. Christensen, Northeast Fisheries Center Sandy Hook Laboratory, National Marine Fisheries Service, NOAA, Highlands, NJ 07732, pers. commun. 1983.

[7]Headboats are vessels which charge anglers for fishing on an individual, thus "per head", basis.

uniform ova size (developmental stage) distribution among anterior to posterior ovarian lobe locations, as has been demonstrated for *Lopholatilus chamaeleonticeps* from the South Atlantic Bight (Erickson et al. 1985).

To determine if the liver was being utilized to store energy in the form of fat reserves to be used in gonad maturation, we calculated a hepatosomatic index (HSI) = liver weight (g)/gutted body weight (g) × 100 (Htun-Han 1978).

Ovaries used to estimate fecundity (= ovarian egg count of Gale and Deutsch (1985)) were preserved in modified Gilson's fixative (Bagenal and Braum 1978). The ovarian tunic was removed and washed free of adhering ova. Developing ova were separated from folicular material and most oogonia by washings under a stream of water. Based upon initiation of yolk accumulation, all oocytes with diameters >0.15 mm were included in ovarian egg counts. Each sample of developing ova was diluted in water and stirred, then at least two subsamples pipetted; each subsample was placed in a 6 × 6 cm gridded Petri dish for counting. Ova were counted in six randomly selected grid squares, and the average number of ova in the six squares was then adjusted to the total subsample count by multiplying the average by the total number of grid squares in the dish. The sample and subsamples were oven dried at 40°C for at least 24 hours and weighed to the nearest 0.001 g on a Mettler[8] balance. Fecundity (total ovarian egg count) was estimated as the number in the subsample multiplied by sample weight divided by subsample weight.

Predictive equations of fecundity from length and weight were fit using least squares regression and converted to functional regressions (Ricker 1973). Fecundity was separately regressed on FL and gutted weight using all possible combinations of untransformed log and semi-log models. We inspected residuals, plots and coefficients of determination to evaluate fits.

RESULTS

Gonad Structure and Sex Determination

Males smaller than 600 mm FL were difficult to sex by gross gonadal structure because testes were small and undeveloped. However, in females larger than about 400 mm FL ovaries were sufficiently developed to visually determine sex easily. Therefore, we histologically examined gonadal tissues of 155 fish (50 males, 545–814 mm FL; 52 females, 241–678 mm FL; and 53 juveniles, 146–400 mm FL). Based upon gonad microstructure, seven fish between 467 and 592 mm FL that were macroscopically unsexable were males. All juveniles and unsexed fish <400 mm FL (79 fish 121–400 mm FL) appeared to be females, i.e., had cell structure consisting of only oogonia. These cells had slightly acidophilic cytoplasm and distinct, but irregular, cell membranes. The nuclear membrane was less obvious because it was masked by basophylic nuclear material located peripherally.

The paired ovaries of adult *L. chamaeleonticeps* are suspended below the swimbladder from the dorsal body wall in the extreme posterior of the body cavity. Ovarian microstructure and development are identical to *Caulolatilus microps* (Ross and Merriner 1983) and *L. chamaeleonticeps* (Erickson et al. 1985) from the South Atlantic Bight and are described in detail by Idelberger (1985).

The testes of tilefish are solid, smooth textured, and more elongate than ovaries. In males smaller than about 65 cm FL, testes were not obviously lobed and were pinkish in color. Only in large adult males were testes creamy white and heavily lobed. Microstructure of the testes was typical of teleosts (Hoffman 1963; Smith 1965; Hyder 1969) and was identical to *C. microps* (Ross and Merriner 1983), and, like the ovary structure, was described in detail by Idelberger (1985). Two males (604 and 609 mm FL) had slight amounts of ovarian tissue within the testicular mass (Fig. 1). That ovarian tissue consisted of several resting or previtellogenic (perinucleolar) oocytes located in testicular mass with definite spermatogenic tubules and crypt structure.

Sexual Dimorphism

The predorsal adipose flap is sexually dimorphic in adult tilefish and can easily be used to determine sex in animals larger than about 70 cm FL. The size of the predorsal flap was significantly larger in males than in females older than age 5 years and larger than 65 cm FL (Table 1). It was not possible to compare predorsal flap sizes of the largest males to those of females, because females do not grow as large as males (Turner et al. 1983; Harris and Grossman 1985).

Sexual Maturity

We determined the general pattern of age and size of sexual maturity using both visual staging and

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

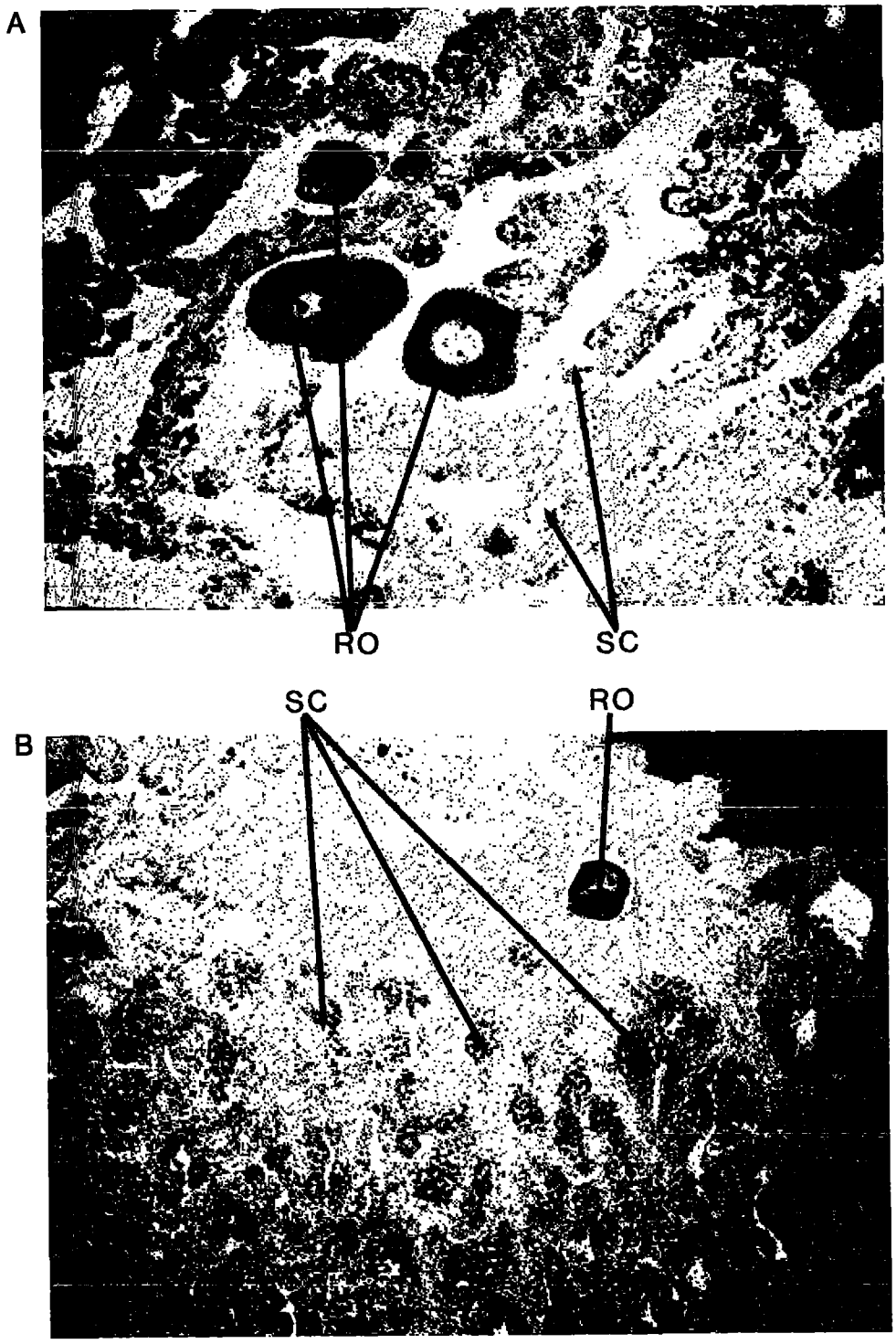

FIGURE 1.—Photomicrographs of histological sections of tilefish testes from a 60.4 cm FL male at ×400 (A) and a 60.9 cm FL male at ×100 (B) showing residual oocytes (RO) and spermatogenic cripts (SC).

TABLE 1.—Mean ($\bar{X}$) and sample size (N) for predorsal adiposal flap height at size and age for male and female tilefish, and students t-tests of flap height differences between sexes.

	Males		Females			
	$\bar{X}$ (mm)	N	$\bar{X}$ (mm)	N	t-value	Probability
Size (FL, mm)						
45–49	20.1	13	17.1	19	1.02	N.S.
50–54	23.1	29	23.6	49	0.33	N.S.
55–59	25.7	36	25.9	62	0.04	N.S.
60–64	30.6	40	27.6	105	0.91	N.S.
65–69	37.1	73	31.6	101	2.63	<0.01
70–74	49.8	67	31.7	51	3.58	<0.01
75–79	61.8	30	37.6	25	4.05	<0.01
80–84	72.3	30	37.7	11	1.90	<0.05
85–89	82.4	12	28.8	8	1.84	<0.05
90–94	68.0	1	38.5	2	Not testable	
95–99	63.0	1	—	0	Not testable	
100–104	98.0	8	—	0	Not testable	
Age (years)						
3	—	0	5.0	6	Not testable	
4	—	0	8.1	7	Not testable	
5	20.5	6	20.4	16	0.018	N.S.
6	36.2	23	21.6	32	6.63	<0.001
7	33.2	41	27.9	51	3.42	<0.01
8	44.0	40	30.1	42	5.64	<0.001
9	51.4	17	30.4	40	5.97	<0.001
10	57.4	8	32.9	35	5.45	<0.001
11	65.0	4	31.9	16	5.59	<0.001
12	—	0	30.9	9	Not testable	
14	—	0	36.5	2	Not testable	
15	112	1	36.8	14	Not testable	

histological data pooled over all years of the study. The two methods gave substantially different results for males; however, both visual and histological data suggested that all females matured at 60–65 cm FL and 8–9 years of age (Figs. 2, 3). Visual staging indicated that virtually all males were mature at 80–85 cm FL and 10–11 years. In contrast, histological results indicated almost all males were mature at 65–70 cm FL (estimated age 7–8 years, Turner et al. 1983) (Figs. 2, 3). That is, visual staging suggested that females matured about 20 cm smaller and 2–3 years younger than males; however, according to histological analysis, both males and females were mature and producing gametes at a similar size (60–70 cm FL). Thus, these results show that although males were producing sperm at 65–70 cm FL (estimated 7–8 years, Turner et al. 1983), they were not developing a large testicular mass until 80–85 cm FL and age 10–11 years.

We reasoned that predorsal adipose flap size might be a sign of maturity or reproductive status of males, because the height of the flap was larger in males than females above 65 cm and age 5 years (see previous section on Sexual Dimorphism). Additionally, the development of enlarged adipose flaps in males coincided with the size of 50% maturity (60–65 cm FL) as judged by development of enlarged testes (i.e., visual method), not at the smaller size of 50% maturity (50–55 cm FL) determined histologically (Fig. 2). Therefore, if predorsal adipose flap height were a sign of reproductive status in males, then mature males should have larger flaps than immature males; and this was so (Fig. 4). Furthermore, ANCOVA (with FL as the covariate) indicated that flap height was significantly larger in mature males than immature males (Table 2).

TABLE 2.—Mean and ANCOVA (with FL as the covariate) of predorsal adipose flap height in sexually mature and immature male tilefish. Flap height data set tested was restricted to a size range containing both mature and immature males (50–75 cm FL). df = degrees of freedom, ss = sum of squares, N = sample size, and $\bar{X}$ = mean.

MEAN			
	N	$\bar{X}$ flap height (mm)	X FL (cm)
Immature	94	28.7	59.4
Mature	87	42.7	68.6

ANCOVA				
Source	df	ss	F	$P > F$
Maturity	1	504.4	6.42	0.0121
FL	1	7,423.4	94.56	0.0001
FL X maturity	1	605.1	7.71	0.0061
Error	177	13,895.7		
Total	180	30,365.8		

Because we had studied reproduction during a period of rapid expansion of the fishery, i.e., the commercial longline fishery had decreased the tilefish population by one-half to two-thirds from 1978 to 1982 (Turner 1986), we decided to examine the data to determine if the fishery had affected the size at which tilefish were developing enlarged testes (i.e., attaining maturity as assessed by the visual method). A comparison of visually assessed sexual maturity at size and age for 1978 and 1982 suggested that females <50 cm FL were maturing at a smaller size in 1978 than in 1982, but that females >50 cm FL matured at very slightly larger sizes in 1978 than in 1982 (Table 3). Log-likelihood contingency tests of these data for females indicated that maturity-at-length was significantly different in 1978 and 1982, but the difference was due to the numbers of mature and immature fish between 41 and 55 cm (Table 3). The data for males <75 cm FL indicated that males matured at smaller size in 1982 than in 1978 (Table 4). A log-likelihood contingency

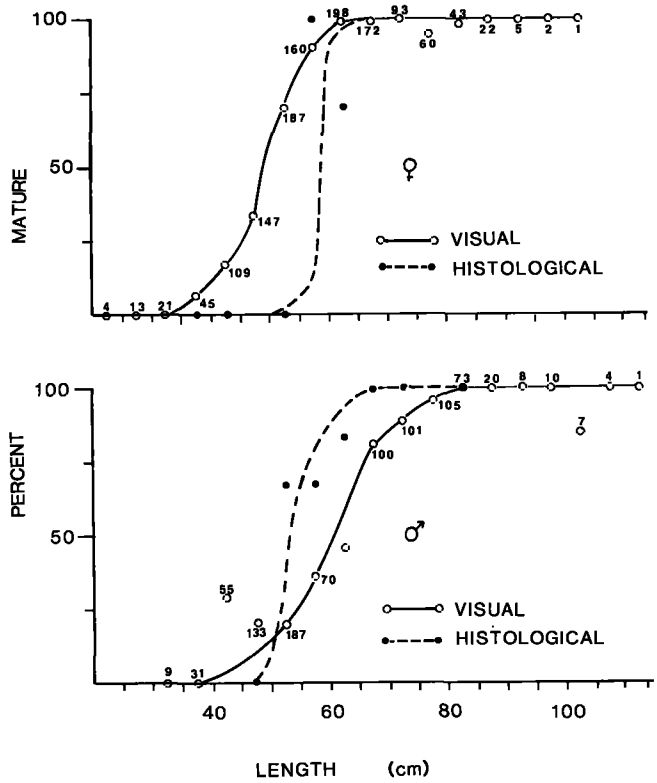

FIGURE 2.—The relationship of sexual maturity (by both visual staging and histological methods) and size (5 cm FL intervals) for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

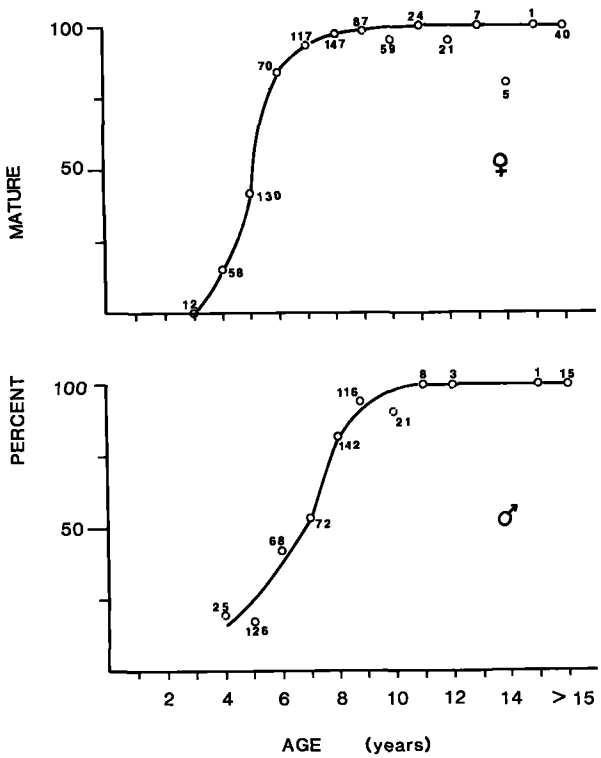

FIGURE 3.—The relationship of sexual maturity (by visual staging) and age for female and male tilefish. Sample size is shown next to each point. Curves are fitted by eye.

TABLE 3.—Female sexual maturity at length (visually determined) and log-likelihood contingency test that maturity at fork length (FL) in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (11 df) = 19.7 and $\chi^2_{0.01}$ (11 df) = 24.7. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
26–30	No data			0	0	1	NT
31–35	0	0	7	0	0	3	0
36–40	3	21	14	0	0	17	0
41–45	11	49	23	4	7	60	30.4
46–50	34	81	42	11	15	72	89.6
51–55	54	59	92	41	89	46	56.5
56–60	40	80	50	35	100	35	0
61–65	63	98	64	49	100	49	0
66–70	57	100	57	27	100	27	0
71–75	12	100	12	29	100	29	0
76–80	12	92	13	14	93	15	0.2
81–85	10	100	10	4	100	4	0
86–90	6	100	6	No data			NT
91–95	3	100	3	1	100	1	0
96–100	No data			1	100	1	NT
Total			393			360	176.7

TABLE 4.—Male sexual maturity at length (visually determined) and log-likelihood contingency tests that maturity at fork length (FL) in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (10 df) = 18.31 and $\chi^2_{0.01}$ (10 df) = 23.2. NT = not testable.

FL (cm)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
31–35	0	0	4	No data			NT
36–40	0	0	15	No data			NT
41–45	5	28	18	11	52	21	4.4
46–50	10	24	42	50	79	63	59.9
51–55	13	12	105	16	43	37	47.3
56–60	0	0	15	19	73	26	0
61–65	8	44	18	12	71	17	5.2
66–70	15	60	25	16	89	18	13.7
71–75	31	79	39	15	94	16	8.9
76–80	47	96	49	20	91	22	1.8
81–85	28	100	28	14	100	14	0
86–90	10	100	10	5	100	5	0
91–95	3	100	3	2	100	2	0
96–100	8	100	8	No data			NT
101–105	3	100	3	No data			NT
106–110	1	100	1	No data			NT
111–115	1	100	1	No data			NT
Total			384			241	141.2

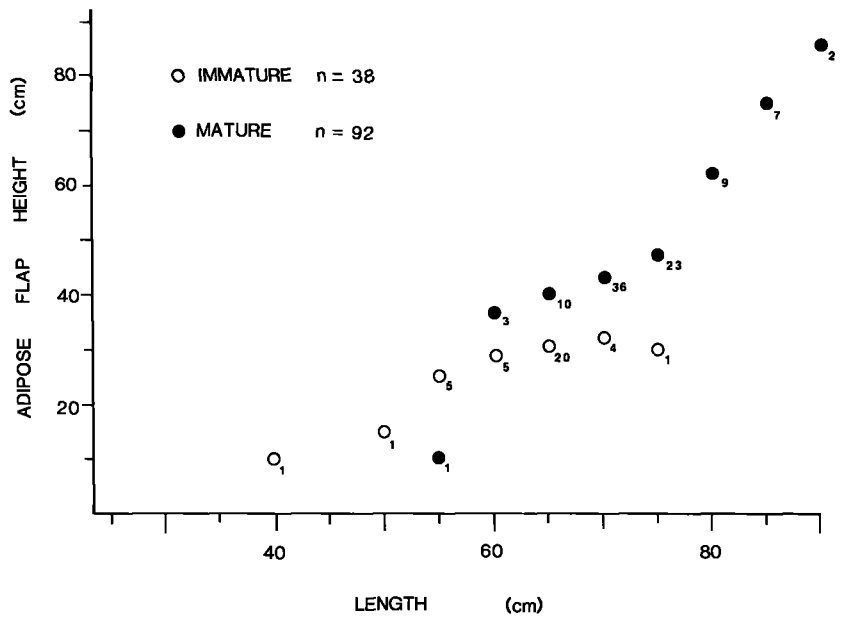

FIGURE 4.—Mean predorsal adipose flap height at length (5 cm FL intervals) for sexually mature and immature male tilefish. Maturity was assessed by visual staging. Sample size is indicated for each interval.

test indicated that maturity-at-age in males for the two years was highly significantly different (Table 4).

Analysis of visual maturity at age data gave less ambiguous results. Percent of females mature at age in 1978 and 1982 was not significantly different (Table 5). However, males matured at younger ages in 1982 than 1978, and the differences between years were highly statistically significant (Table 6).

TABLE 5.—Female sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in female tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (9 df) = 16.9 and $\chi^2_{0.01}$ (9 df) = 21.7. NT = not testable.

Age (yr)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
3	0	0	1	0	0	3	0
4	1	8	13	1	5	19	0.3
5	35	43	82	5	33	15	3.1
6	19	83	23	3	75	4	0.6
7	47	90	52	8	100	8	0
8	68	97	70	20	95	21	0.7
9	14	100	14	14	100	14	0
10	2	100	2	12	100	12	0
11	No data			7	100	7	NT
12	1	100	1	8	100	8	0
13	No data			4	100	4	NT
14	No data			2	100	2	NT
≥15	9	100	9	4	100	4	0
Total			267			121	4.7

TABLE 6.—Male sexual maturity at age (visually determined) and log-likelihood contingency tests that maturity at age in male tilefish was not different for 1978 and 1982. Critical chi-square values are $\chi^2_{0.05}$ (8 df) = 15.5 and $\chi^2_{0.01}$ (8 df) = 20.1. NT = not testable.

Age (yr)	1978 Maturity No.	1978 Maturity %	1978 Sample size	1982 Maturity No.	1982 Maturity %	1982 Sample size	G-statistic
4	1	6	16	3	75	4	34.5
5	10	10	96	7	41	17	44.8
6	3	19	16	8	80	10	27.6
7	6	38	16	6	75	8	22.3
8	41	77	53	15	75	20	0.6
9	23	85	27	19	100	19	0
10	5	100	5	6	86	7	0
11	2	100	2	1	100	1	0
12	1	100	1	2	100	2	0
≥15	11	100	11	No data			NT
Total			246			88	129.8

TABLE 7.—Sex ratio at length and log-likelihood tests that sex ratio was not different from 1:1 at 5 cm FL intervals. All G scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Fork length (cm)	Number of females	Percent	Number of males	G-statistic
46–50	46	46	54	0.6
51–55	95	41	134	6.7
56–60	56	78	16	23.5
61–65	66	78	19	27.5
66–70	74	69	33	16.1
71–75	18	30	43	10.5
76–80	14	21	53	25.8
81–85	13	30	31	7.6
86–90	7	37	12	1.3
91–95	5	63	3	0.4
96–100	0	0	9	NT
101–105	0	0	4	NT
106–110	0	0	2	NT
111–115	0	0	1	NT

Sex Ratio

To minimize the chances of obtaining biased results caused by the effects of fishing we estimated sex ratio at size and age using only data collected in 1978 when the tilefish population was lightly exploited. Proportions of males and females were similar in the 46–50 and 51–55 cm FL intervals, although the ratio in the 51–55 cm FL interval tested significantly different at $P < 0.05$ (Table 7). Males were significantly predominant (70–80%) between 71 and 90 cm FL. At the 91–95 cm FL size females were predominant once again (>50%), although not significantly so (Table 7). Above 100 cm FL only males were collected.

The general pattern of sex ratio at age in 1978 seems to have been equal proportions of the sexes through about age 20 years, with only females present from ages 29 to 36 years. Log-likelihood tests of sex ratio at age showed no significant differences from equality except for ages 7 and 8 years; sex ratio at age was not testable for ages 29–36 years because only females were present (Table 8).

Although sex ratio was skewed with age and size, the estimated sex ratio for the entire population was different from 1:1 in 1978 (Table 9). We calculated the population to be 46.2% males, and could not reject the null hypothesis that sex ratio is not different from 1:1 ($\chi^2 = 0.15$, df = 1, $\chi^2_{0.05} = 3.84$) in the population ≥50 cm FL.

Spawning

Several lines of evidence suggest that tilefish in the Mid-Atlantic–southern New England area are

TABLE 8.—Sex ratio at age and log-likelihood tests that sex ratio at age was not different from 1:1. All *G* scores were calculated using Yates correction for small sample sizes. Critical chi-square values are $\chi^2_{0.05}$ (1 df) = 3.84 and $\chi^2_{0.01}$ (1 df) = 6.64. NT = not testable.

Age (yr)	Number of females	Percent	Number of males	*G*-statistic
4	1	100	0	NT
5	43	46	50	0.7
6	10	67	5	2.5
7	40	78	11	18.8
8	69	62	42	7.1
9	20	49	21	1.0
10	2	29	5	2.4
11	0	0	2	NT
16	2	40	3	0.8
19	2	50	2	Equality
29	1	100	0	NT
30	1	100	0	NT
31	1	100	0	NT
32	2	100	0	NT
33	1	100	0	NT
34	1	100	0	NT
35	1	100	0	NT
36	1	100	0	NT

TABLE 9.—The proportion of male tilefish in the 1978 population ≥50 cm FL, $P = \sum_{i}^{n} L_i M_i$ where *L* and *M* = the proportion of all fish and males, respectively, in the i^{th} 5 cm FL interval, and *n* = the number of size intervals. L_i was determined from the 1978 commercial longline catch of tilefish.

Fork length (cm) *i*	Proportion of all fish *L*	Proportion of males *M*	Proportion of males in population *P*
<50	0.026	0	0
51–55	0.058	0.540	0.032
56–60	0.158	0.253	0.026
61–65	0.073	0.167	0.012
66–70	0.162	0.267	0.044
71–75	0.191	0.646	0.127
76–80	0.110	0.792	0.089
81–85	0.087	0.744	0.066
86–90	0.682	0.611	0.043
91–95	0.021	0.400	0.008
96–100	0.011	0.875	0.010
≥101	0.036	1.000	0.004
			= 0.462

fractional spawners from about March through November, although most of the reproduction evidently occurs from May to September. Some females with free ova in the ovarian lumen (running ripe) were present in March through August and in October and November. From May through August, 89–98% of the females were ripe or running ripe (Fig. 5). Running ripe or ripe males were not as frequently observed as were females in a similar reproductive state. In fact, only very large males (75–80 cm FL) were observed with a large creamy white swollen testicular mass. Ripe males were found in January, March, May through August, October, and November, but the highest proportions (23–46%) were present in May through August (Fig. 5).

GSI data for females indicated a similar seasonal spawning pattern (Fig. 6). Highest GSI values consistently occurred from May through August, when ovaries accounted for 3.5–8.3% of gutted body weight.

Analysis of ovum-diameter data also suggested that spawning occurred mostly from May to September, and indicated that spawning was fractional, i.e., ova were released in batches. Highest monthly mean developing ovum diameters (0.30–0.42 mm) occurred in May through August (Fig. 7). During these months mean ovum diameter was usually >0.35 mm (Fig. 7). During other months, mean ovum diameter was always ≤0.30 mm. The size-frequency distribution of ova from running ripe females was polymodal (Fig. 8), suggesting multiple spawnings by individual females during the reproductive season.

Tilefish may not utilize the liver and soma to store energy as fat for mobilization to the gonads in preparation for spawning as many species are thought to do (Hoar 1957). HSI for both males and females showed a distinct pattern of seasonal variation, but highest values occurred during summer (spawning season) and lowest in winter (Fig. 9). Somatic condition factor (eviscerated weight, g/FL^3) showed no discernable seasonal pattern in males or females.

Fecundity

Because tilefish are fractional spawners, fecundity (ovarian egg count) was estimated from females collected early in the spawning season (i.e., May to early June) to minimize the chance of using a partially spawned ovary and underestimating egg number. Estimates of fecundity ranged from approximately 195,000 for a 53 cm FL (2.1 kg) female to 10 million for a 91 cm FL (13 kg) female, with a mean egg count of 2.28 million (n = 49, SD = 1.02). The 91 cm FL female with 10 million eggs was exceptional; all other estimates were <4.1 million, even for other large females 80 and 86 cm FL. Therefore, we judged that the two largest fish, 91 and 86 cm FL, were outliers and developed predictive equations for egg count without using outlier data.

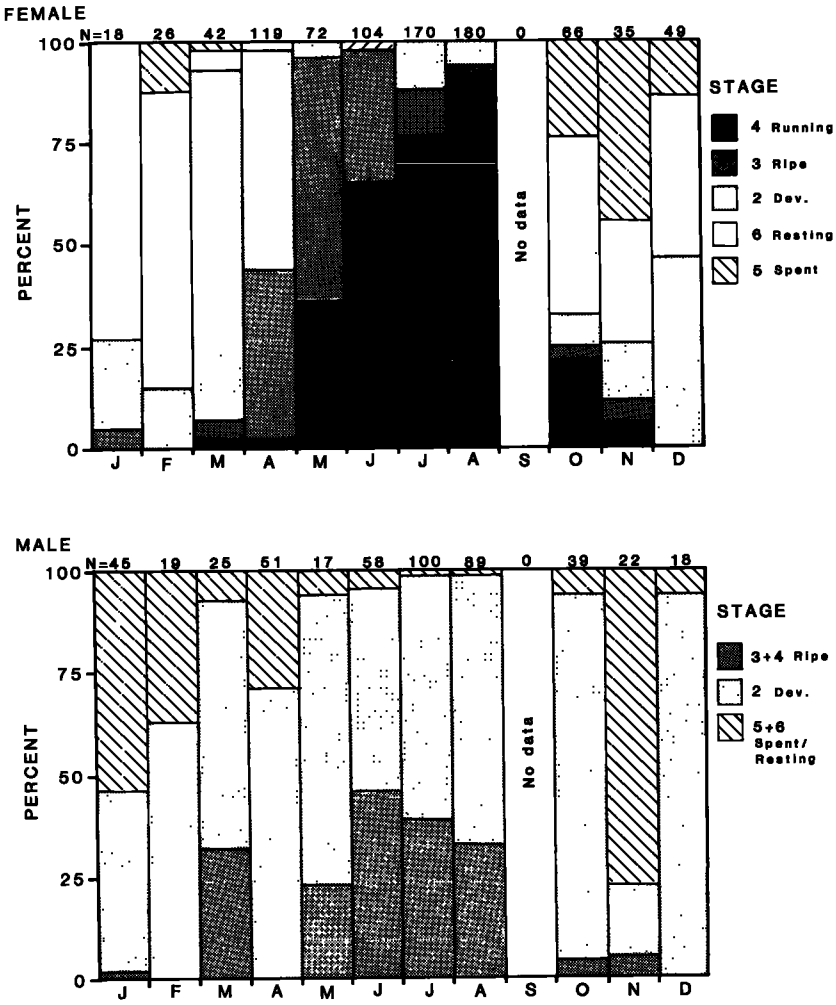

FIGURE 5.—Reproductive seasonality of female and male tilefish as indicated by the percent of various visual maturity stages collected by month from 1978 to 1982.

Log-transformed models produced slightly superior fits, with length proving a slightly better predictor of ovarian egg count than weight ($\log_e Y = 4.75 \log_e FL - 5.2$, $r^2 = 0.62$, $n = 48$; $\log_e Y = 1.48 \log_e W + 2.48$, $r^2 = 0.59$, $n = 48$). Based upon our estimates, a first spawning female would produce <500,000 eggs.

DISCUSSION

Seasonality and Spawning

It seems clear that the northern stock of *Lopholatilus chamaeleonticeps* consists of fractional spawners over an 8 or 9 month season, with peak spawning from May to September. Our findings agree with the limited information previously reported. Collins (1884) reported ripe fish in July; Bigelow and Schroeder (1953) in August; Dooley (1978) in February, March, June, and July; Morse (MS)[9] March through August; and Freeman and Turner (1977) from mid-March to mid-September. Other members of the Branchiostegidae (*Caulolatilus microps*, *C. chrysops*, *C. princeps*, *C. affinis*,

[9]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

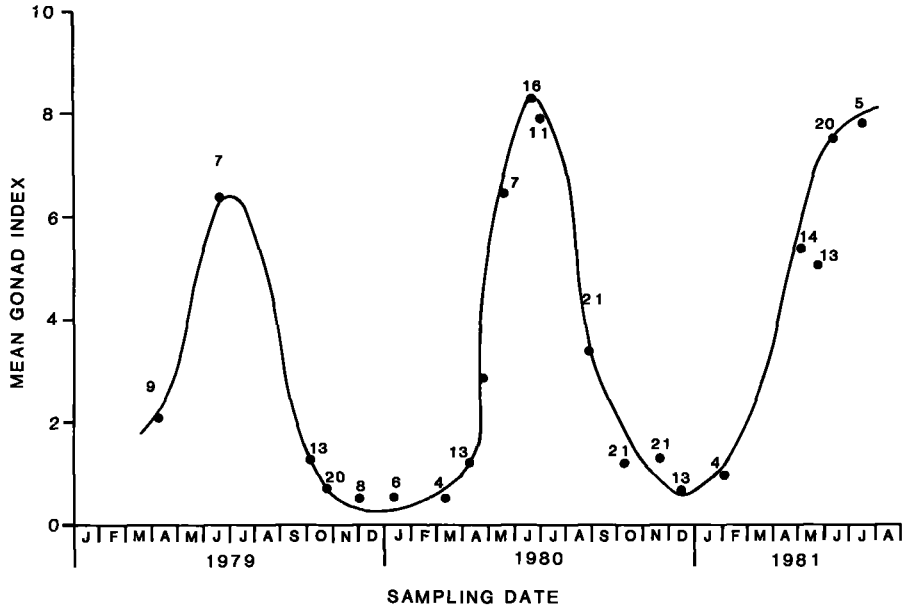

FIGURE 6.—Reproductive seasonality of female tilefish as indicated by monthly mean gonad index. Sample size is indicated for each month.

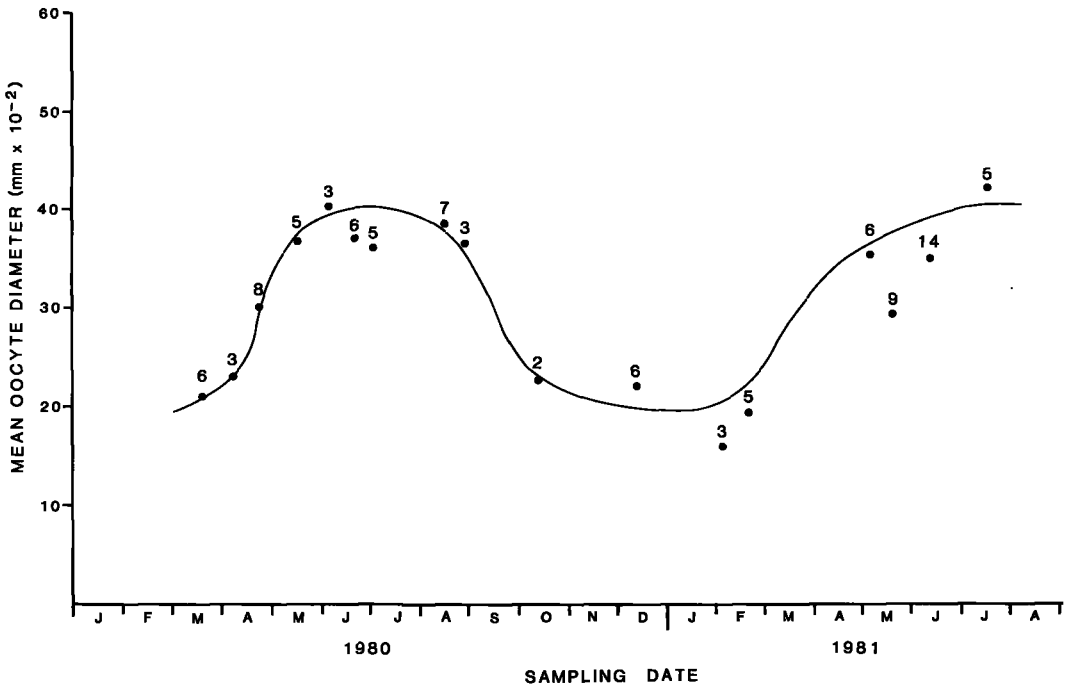

FIGURE 7.—Reproductive seasonality of female tilefish as indicated by monthly mean oocyte diameters. Sample size is indicated for each month.

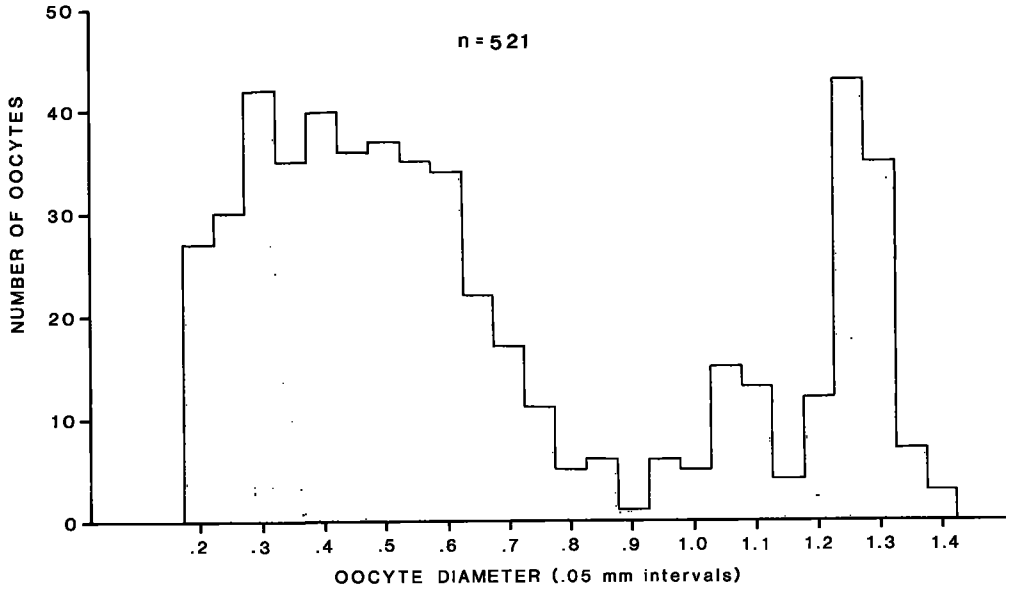

FIGURE 8.—Frequency distribution of oocyte diameters from a spawning 66 cm FL female tilefish (running ripe) collected in June 1979.

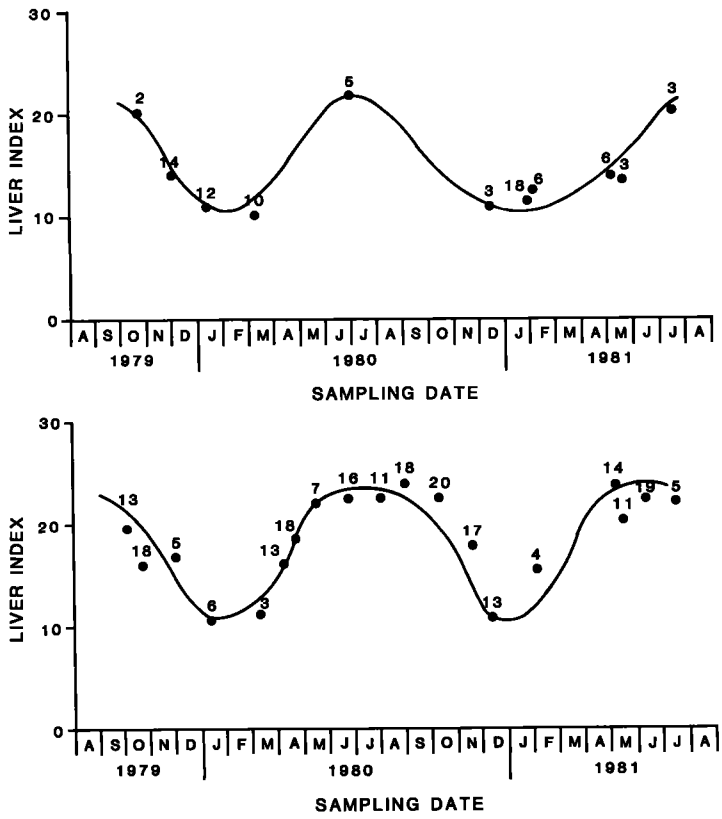

FIGURE 9.—Monthly mean heptosomatic index for male (upper) and female (lower) tilefish. Sample size is shown next to each mean.

Branchiostegus japonicus) all exhibit extended reproductive seasons centered around summer (Hayashi 1977, 1979; Dooley 1978; Ross and Merriner 1983). However, Erickson et al. (1985) reported that *L. chamaeleonticeps* spawned from March through June off Georgia in the South Atlantic Bight. The reason for the shorter reported spawning season for *L. chamaeleonticeps* in the South Atlantic Bight is uncertain.

Fractional spawning by individual females was indicated by the polymodal frequency distribution of ovum diameters. This asynchronous follicular development is typical of fractional spawning (deVlaming 1983), and has been reported for *L. chamaeleonticeps* in the South Atlantic Bight (Erickson et al. 1985) and Mid-Atlantic Bight (Morse fn. 9). Fractional spawning based upon polymodal ovum-diameter distributions has also been reported for the confamilials *C. microps* and *B. wardi* (Dooley 1978; Ross and Merriner 1983).

Our estimates of fecundity in tilefish are consistent with those in the literature. We agree with Gale and Deutsch (1985) that the term fecundity is incorrectly applied to many fishes, especially fractional spawners, because in most cases there is no reasonable means to determine which or how many oocytes or developing ova will be released, or how many ovarian ova will be resorbed after spawning and never released. Therefore, we recognize that our ovarian egg count data provides only a rough estimate of actual fecundity. Erickson and Grossman (1986) found the relationship between fecundity and weight to be best described by a log transformation ($\log_e F = 1.497 \log_e W + 12.59$, $r^2 = 0.93$); while Morse (fn. 9) found the relationship best fitted to a linear form ($F = -966{,}471 + 887\ W$, $r^2 = 0.61$). To compare our estimates further we calculated relative fecundity using extreme point estimates of fecundity reported by other authors (Erickson and Grossman 1986, $414 \cdot g^{-1}$ and $950 \cdot g^{-1}$ for 2.0 and 8.0 kg fish; Morse fn. 9, $543 \cdot g^{-1}$ and $867 \cdot g^{-1}$ for 3.5 and 9.0 kg fish) and this study ($119 \cdot g^{-1}$ and $769 \cdot g^{-1}$ for 2.1 and 13.0 kg fish), and using predictive equations (Table 10). Comparing the range of point estimates, the three studies are similar, however our findings agree more closely with Erickson and Grossman (1986) when the comparison is based upon predictive equations. The inconsistency in the comparison is because Morse (fn. 9) used a linear equation, thus assuming that egg production per gram of body weight was constant for all body weights, and Erickson and Grossman (1986) and this study chose curvilinear equations. It is possible to conclude that small tilefish, like some other fishes (Grimes 1987), produce fewer eggs per unit body weight than larger fish.

We compared numbers of ova actually found in ripe ovaries collected on 1 July ($n = 3$) and 28 August ($n = 6$) to ovarian egg numbers predicted for the same size females to estimate what proportion of ova had been spawned in the mid- and late-spawning season. The analysis suggested that approximately 25% of ovarian eggs were spawned by July and 50% by the end of August. The ovaries of two postspawning females collected on 10 October contained considerable quantities of ovarian eggs >0.15 mm in diameter. These ova accounted for 15–20% of the predicted ovarian egg number. By December 11 ($n = 3$) the number of ovarian eggs >0.15 mm in diameter had decreased to about 5% of the predicted maximum ovarian egg number. Since atretic ova were observed in histological preparations of ovaries in spent and resting stages, and resorption is well documented in other teleosts (Hoar 1957; Smith 1965; Combs 1969; Foucher and Beamish 1977; LaRoche and Richardson 1980; Waltz et al. 1982), it seems reasonable to conclude that at least 15–20% of the maximum ovarian egg number are never spawned and are resorbed during the winter.

Sexuality

Our results agree with Erickson and Grossman (1986) that tilefish are gonochoristic and that secondary gonochorism is a possibility. Gonad microstructure and development of adult (>50 cm FL) tilefish were typical of most male and female oviparous teleosts, and identical to that described for

TABLE 10.—Comparison of ovarian egg number and relative ovarian egg number for small (2.0 kg) and large (9.0 kg) female tilefish calculated following Erickson and Grossman (1986), Morse,[1] and this study.

	Body weight	Egg number	Relative egg number
Erickson and Grossman	2.0	828,723	414
	9.0	7,875,326	875
Morse	2.0	1,773,003	887
	9.0	7,982,003	887
This study	2.0	917,434	459
	9.0	8,498,245	944

[1]Morse, W. W. Length, weight, spawning and fecundity of the tilefish, *Lopholatilus chamaeleonticeps*, from New Jersey waters. Unpubl. manuscr. Northeast Fish. Cent. Sandy Hook Lab., Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732.

male and female *Caulolatilus microps* (Ross and Merriner 1983) and female *Lopholatilus chamaeleonticeps* (Erickson et al. 1985). Like Ross and Merriner (1983) and Erickson and Grossman (1986), we also found a few adult males (2 of 50) with ovigerous tissue (previtellogenic residual oocytes) in the testicular mass. Histological sections of testes revealed no gross structural features that indicated prior functional female status (e.g., remnants of an ovarian lumen (Sadovy and Shapiro 1987)). Furthermore, no ovary was ever observed in transition to a testis (transitional ovotestes), however transition can occur within a matter of weeks. Similar to other branchiostegids (*C. microps*, Ross and Merriner 1983; *Branchiostegus wardi* and *B. serratus*, Dooley 1978; *L. chamaeleonticeps*, Erickson and Grossman 1986), sex ratios were skewed in favor of males at large sizes. However, both sexes were present at most sizes and ages (45–95 cm FL and 5–10, 16, and 19 years) and only females were present at ages 29–36 years, ruling out protogyny. Disparate sex ratios at size are apparently due to differential growth and mortality rates between sexes (Turner et al. 1983; Harris and Grossman 1985).

Our histological examination of juvenile gonads suggest that some *L. chamaeleonticeps* may undergo prematurational sex reversal. All juvenile gonads examined (63 fish, 146–400 mm FL) appeared to be female, based upon gonad cell structure (i.e., presence of only oogonia and previtellogenic oocytes). We are very tentative about the determination that all of these small fish (<400 mm FL) were females, because undifferentiated gonia, oogonia, and spermatogonia are very similar in appearance (Yamamoto 1956; Hoffman 1963; Hyder 1969; Ross 1978). Once a gonad has developed gross structure such as spermatogenic tubules and crypts, or an ovarian lumen, determining sex is straightforward. We found residual oogonia in 2 of 50 histologically examined testes. We found no juveniles with truly intersexual gonads, nor were we able to observe a lumen. Ross and Merriner (1983) suggested that the confamilial *C. microps* underwent prematurational sex reversal, and that gonochorism in *C. microps* might be a regression from monandric protogyny. Their conclusions were based upon findings from four juveniles (one specimen with a totally ovarian gonad and the remaining three with gonads that contained substantial amounts of testicular tissue), and adult males (8 of 41 examined) with residual oocytes in the testicular mass.

That prematurational sex reversal has been observed among several families and species of fish suggests that either prematurational sex reversal is more common among fishes than suspected, or that early gonad development in fishes involves an all-female or female-appearing stage. For example, the salmonid *Salmo gairdneri* (Mrsic 1923); the cyprinids *Brachydanio rerio* (Takahashi 1977), *Barbus tetrazona* (Takahashi unpubl. data cited in Takahashi 1977), *Rodeus ocellatus* (Shimizu 1979), *Cyprinus carpio* (Davis and Takashima 1980), and *Carassius auratus* (Stromsten 1931; Takahashi and Takano 1971); and the anabantids *Macropodus concolor* and *M. opercularis* (Schwier 1939) are hatched as all females having ovaries with no testicular characteristics. About one-half continue normal development to mature females and about one-half undergo a transitory intersexual stage before becoming adult males. The female juvenile cyprinids *Brachydanio rerio*, *Barbus tetrazona*, *Rhodeus ocellatus*, and *Carassius auratus* all develop an ovarian lumen, as well as oogonia and previtellogenic oocytes. Prematurational sex change is reportedly common among the hermaphroditic Sparismatinae (Scaridae) that spend their entire life as males (Robertson and Warner 1978).

Social Control

We interpret the data on sexual maturity and sexual dimorphism to suggest that some sexually mature males delay participation in spawning for up to 3 years and 10–15 cm, and that this mating system is socially mediated. Histological assessments of sexual maturity revealed that both males and females produced mature gametes by about 50 cm FL and 5–6 years. However, visual inspection of gonads to determine maturity gave the same result as the histological evidence in females, but indicated that males were not mature until attaining 65–70 cm FL and 7–8 years. Ross and Merriner (1983) also reported that some *Caulolatilus microps* males that were visually assessed as immature were later shown by histological methods to be producing mature gametes, and Erickson and Grossman (1986) found *L. chamaeleonticeps* off Georgia that showed active, yet incomplete spermatogenesis.

Sexual dimorphism in tilefish is manifested in the size of the adipose flap which is conspicuously larger in males than females and larger ultimate body size in males; size of the adipose flap may be an indication of male breeding status. The adipose flap of males became larger at 65–70 cm FL (7–8 years) when males were judged sexually mature by visual inspection (i.e., had developed large testes), not

when they were functionally mature at 50 cm FL as revealed by histological methods.

A nonrandom mating system of pairing, involving mate selection by females, is consistent with the both sexual dimorphisms observed in tilefish. Female mate selection can convey a reproductive advantage to large males (Ghiselen 1969; Howard 1979), but in randomly mating species, females are usually larger than males (Ghiselen 1969). Female ability to discriminate males is required to support female mate selection (Howard 1979), which often leads to development of specialized structures and colorations by males for display (Krebs 1972; Warner and Robertson 1978). The enlarged adipose flap in tilefish certainly represents a conspicuous, highly visible feature in some adult males that could serve as a visual cue to signal male breeding status.

The evolution of a female mate selection system requires that a male have the ability to control resources important to the female (Howard 1979; Krebs and Davies 1984), and several lines of evidence suggest that male tilefish may be territorial. Burrowing is apparently the rule in the family (Able et al. 1987). Direct observation from submersibles and mark-recapture data indicated that tilefish orient to particular burrows, and may be long-term residents of their habitats (Grimes et al. 1983, 1986). Furthermore, time-lapse photography showed the same male-female pair of tilefish utilizing the same burrow over a 26-h period (Grimes et al. 1986), and pair formation has been observed in the branchiostegids *Malacanthus plumieri* (Clark and Ben-Tuvia 1973), *Hoplolatilus* sp. (Thresher 1984), and *H. starcki* and *H. cuniculus* (Randall and Dooley 1974).

We believe that our data indicate that tilefish have a mating system consisting of two classes of sexually mature males, a category actively engaged in spawning and a category of satellite males that do not spawn. Similar breeding systems have been described for several species of hermaphroditic reef fish (Popper and Fishelson 1973; Fishelson 1975; Warner and Robertson 1978; Robertson and Warner 1978; Warner and Hoffman 1980; Shapiro 1984). For example, there are scarid and labrid populations with large territorial terminal phase males that have preferred mating status, and nonterritorial initial phase males that have nonpreferred breeding status (Warner and Robertson 1978; Robertson and Warner 1978). Hermaphroditic populations of the serranid *Anthias squamipinnis* in the Gulf of Eilat have two behaviorally distinct types of males, a dominant territorial male that actively courts, interacts, and spawns with females, and smaller males that do not interact or spawn with females in the social group. The latter male category have filamentous degenerative gonads (Popper and Fishelson 1973; Fishelson 1975). These mating systems are characterized by strong sexual selection and maintenance of reproductive territories by males, and by being reef systems in which fish are habitat limited. Tilefish are also severely habitat limited, i.e., to burrowable clay substrate generally (Able et al. 1982; Grossman et al. 1985; Grimes et al. 1986).

During the period we studied reproduction, the fishery for tilefish was rapidly expanding, and one effect of fishing seems to have been to alter the structure of the mating system. Based upon both age-structured and non-age-structured population modeling, tilefish population density was reduced by about one-half to two-thirds from 1978 to 1982, apparently due to the rapid expansion of the commercial longline fishery (Turner 1986). Female size, and particularly age, at maturity do not seem to have been altered in any consistent fashion by the population reduction from fishing. Males, on the other hand, appear to have experienced profound changes in visually assessed maturity; they clearly were mature at smaller size (10 cm) and younger age (2–2.5 years) in 1982 than in 1978.

We interpret the decrease in size/age of maturity in males to be the effect of fishing. Fishing lowered population density, and in so doing may have made mating territories available to smaller and younger males. This interpretation is supported by the findings of Warner and Robertson (1978) and Robertson and Warner (1978) that the ratio of the two categories of sexually mature males (initial and terminal phase) in western Caribbean scarid and labrid populations was density dependent; i.e., relatively more initial phase males were found in dense populations.

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A FIELD METHOD FOR DETERMINING PREY PREFERENCE OF PREDATORS

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ABSTRACT

A new field method for determining prey preferences of fish that feed on juvenile salmon is described. The basic elements of this method consist of capturing, tagging or marking, and releasing prey with known characteristics, and comparing these characteristics with those of tagged prey subsequently recovered from the stomachs of predators. The feasibility of this approach is illustrated by two experiments conducted in 1985, designed to assess prey size preferences of predators feeding on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon, *Oncorhynchus kisutch*, were size selective when feeding on juvenile pink salmon, *O. gorbuscha*, preferring the smaller prey. A major advantage of this method is that it eliminates the need to determine the abundances of various prey types in the field. It also allows the investigator to control or precisely measure many of the variables that are known to affect the availability of prey to predators.

Predation plays an important role in shaping the ecological structure of many biological systems. One aspect of predation that has attracted considerable interest is the observation that, when offered a choice of prey types, predators typically show a preference for one of them. The result is that more of the preferred prey are consumed than would be expected, based on the relative abundances of the various prey types.

There have been many attempts to quantify the food or prey preferences of predators (e.g., Hess and Swartz 1940; Ivlev 1961; Schneider 1981) using a wide variety of mathematical indices of preference (reviewed by Cock 1978; Pearre 1982). In some situations, however, this approach clearly is not suitable. For example, in many systems the relative abundances and species composition of the prey can vary substantially over the normal feeding range of the predators. This is particularly evident in fisheries, where piscivorous predators and their prey are often very mobile, and can travel considerable distances during even a single feeding period. In such cases, the proportions of the various prey found in the stomachs of predators may result from variations in the relative concentrations or availability of prey over the extensive area searched by the predator, rather than from any prey preference. It is typically very difficult to determine the concentrations and species composition of prey over such large areas, so indices of preference may not provide much insight into the predation process.

The purpose of this paper is to describe a new method for determing the prey preference of predators in the wild. This method consists of a field experiment in which a number of potential prey with known characteristics are released. These prey are tagged prior to release to allow positive identification even if they mix with other prey of the same type after they are released. The prey preference of the predators is assessed directly by comparing the characteristics of the tagged prey found in the stomachs of predators with those of the prey that were released. The major advantage of this approach is that the relative abundances and other characteristics (species ratios, size composition, etc.) of the various prey types are known in advance and additional field measurements are not required. In addition, if only tagged prey are compared, there is much less ambiguity in assessing the preference of predators for each type of prey because the major alternative explanations are eliminated. Although applicable to a wide variety of predator-prey interactions, the details and potential utility of this method are illustrated by two experiments conducted in Masset Inlet and Masset Sound, B.C., Canada. In both cases the goal was to test the hypothesis that natural fish predators were size selective when feeding on juvenile pink salmon, *Oncorhynchus gorbuscha*, during the early sea-life period.

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METHODS

The first experiment was conducted on 26 April and the second experiment during 6 and 7 June 1985. Pink salmon fry were captured in the Yakoun River during 10–18 April using two inclined plane traps with mouth openings of 1.1 m^2. The traps were emptied each morning and the pink salmon transferred by truck to several 1 m^3 net pens attached to the research vessel *Velella*, anchored at Marinelli Point (Fig. 1).

All pink salmon were tagged and marked to allow positive identification after they were released. During 15–18 April 6,000 pink salmon were anesthetized with tricaine-methanesulfonate (MS-222) and tagged with half-length binary-coded wire tags by an experienced tagging crew. Proper placement of each tag was confirmed by passing all fish through

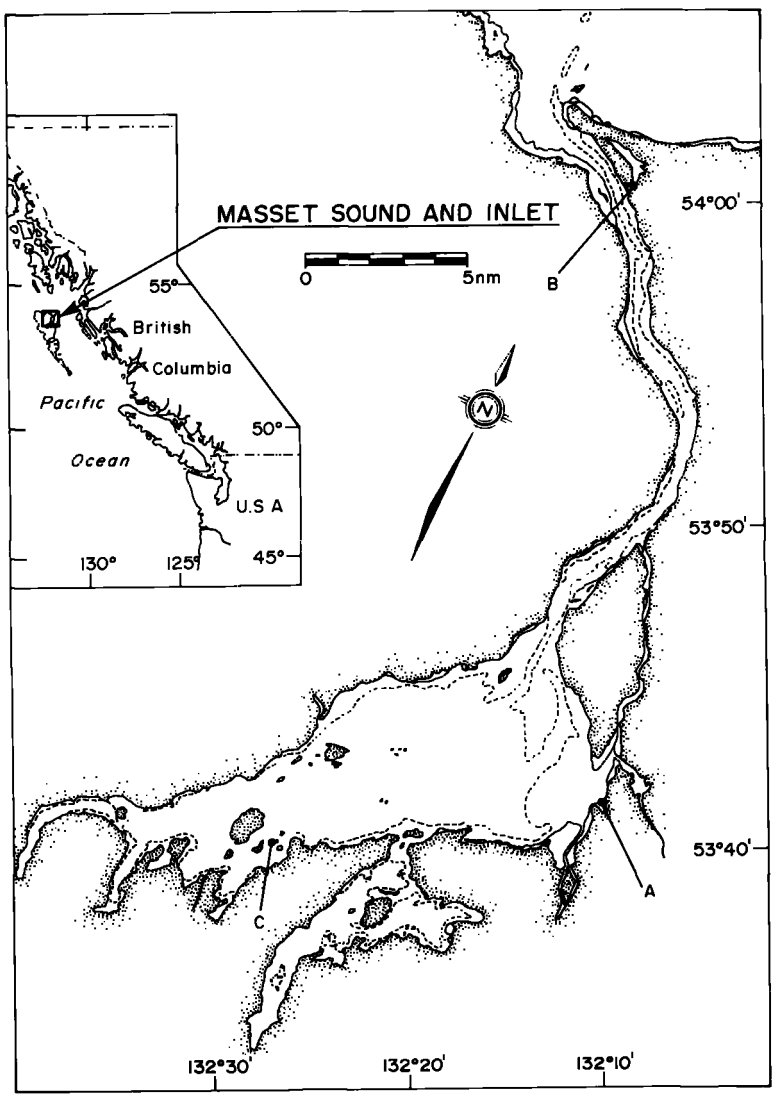

FIGURE 1.—Chart of Masset Inlet showing locations of first (Marinelli Point) (A) and second (B) releases of tagged fish and saltwater enclosure (C) used to hold tagged fish until required for the second experiment.

a 2.54 cm (1 inch) diameter Quality Control Device (QCD), manufactured by Northwest Marine Technology[2] (Shaw Island, WA 98286). Samples of tagged fish were also dissected and examined visually and microscopically to verify tag implantation. Three thousand of these pink salmon were also marked externally by amputating either the left or right pectoral fin. No other fins were amputated. The purpose of the fin clipping was to determine which method (nose tag or fin clip) was more effective for identifying fish recovered from the stomachs of predators.

After tagging and marking, all pink salmon were transferred back into the small, saltwater enclosures. On 20 April the three thousand tagged but unmarked pink salmon were transferred to a larger (51 m^3) enclosure anchored near the southwest end of Masset Inlet, and held until required for the second experiment. This enclosure was shallowed by hand once each week to check the condition of the fish and cleaned with a high-pressure hose every 10–14 days to remove algae growing in the meshes. The food supply of the pink salmon held in this enclosure was not controlled and consisted of whatever came through the meshes. No supplementary food was added. Under this regime the pinks remained very active and appeared healthy.

The first experiment was initiated at 1600 on 26 April, by releasing 3,000 tagged and fin-clipped pink salmon at Marinelli Point. A sample of 99 fish was removed, anesthetized with 2-phenoxyethanol, and the live fork length of each fish measured to determine the size distribution of fish at the time of release. A single beach seine set was made three hours later, in the immediate vicinity of the release site, to collect a sample of potential predators.

The second experiment was initiated by releasing 1,800 tagged pink salmon at 1130 on 6 June, into the boat harbor at Masset (Fig. 1). None of these fish were fin-clipped. A sample of 100 pink salmon was removed prior to the release, and each fish measured to determine the size distribution of fish at the time of release. Two beach seine sets were made to collect potential predators prior to the time of release, the first at 0930 and the second at 1015. A total of sixteen additional sets were made after the release, seven between 1245 and 1826 on 6 June, and nine more between 0900 and 1400 the following day.

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

The beach seine used to capture potential predators was 46 m long and constructed of 6.4 mm stretched nylon mesh. All potential predators were examined immediately after capture. Each measured fish was anesthetized in 2-phenoxyethanol, and the stomach contents obtained by either hydraulic flushing or dissection. All fish remains in the stomach contents were examined visually or microscopically to identify prey to the species level, using Hart (1973) as a general reference and Phillips (1977) to identify juvenile salmon. All juvenile salmon found in the stomachs of predators and any live juvenile salmon captured along with the predators were measured (if possible), examined for missing fins, and passed through the QCD several times to determine if they were tagged.

Yearling coho salmon, *Oncorhynchus kisutch*, captured on the first day of the second experiment were used to obtain an estimate of the total population of coho salmon in the vicinity of the release site. All coho salmon captured on 6 June were retained, anesthetized with 2-phenoxyethanol, and marked using a hot-wire branding device. At 2000 on 6 June, these coho were sorted to remove any that did not appear healthy and fully recovered, and the remaining 170 were released. All coho captured the following day were inspected to determine if they were marked. The numbers of marked and unmarked coho were used to derive a simple (single census) Petersen estimate of the total population of yearling coho salmon in the vicinity of the release site using the following equation (Ricker 1975):

$$N = \frac{(M + 1)(C + 1)}{(R + 1)} \quad (1)$$

where N = total number of coho salmon at time of marking
M = number of coho salmon marked and released on 6 June
C = total number of coho salmon captured on 7 June
R = number of marked coho salmon recaptured on 7 June.

The 95% confidence interval for the population estimate was obtained by substituting into this equation the fiducial limits of the number of recaptured coho salmon, from tables of the Poisson distribution (Ricker 1975). These figures were used to estimate the total number of tagged pink salmon eaten by coho salmon in the second experiment, using the equation

$$T = (P * N)/E \quad (2)$$

where T = total number of pink salmon eaten
P = total number of pink salmon in all stomachs examines
N = estimated total population of coho salmon, from Equation (1)
E = total number of stomachs examined.

RESULTS

The 3,000 tagged and marked pink salmon released at Marinelli Point on 26 April ranged in size from 34 mm to 41 mm, with an average of 38 mm (Table 1). A total of 57 juvenile sockeye salmon (*Oncorhynchus nerka*), 5 pink salmon, 2 chum salmon (*O. keta*), 4 starry flounder (*Platichthys stellatus*), 1 sturgeon poacher (*Agonus acipenserinus*), and 210 yearling coho salmon were captured in the single beach seine set done after the tagged fish were released. All five pink salmon had been fin-clipped and tagged. Three of these pinks had fork lengths of 37 mm and the other two were both 38 mm long. The two chum salmon had fork lengths of 41 mm and 40 mm. The four starry flounders and single sturgeon poacher were all small and were immediately released. All 210 coho salmon were measured and their stomach contents examined for evidence of predation on juvenile pink salmon. A total of 90 coho salmon had remains of fish in their stomachs, including 51 pink salmon, 1 chum salmon, and 14 juvenile salmon that could be identified only as either pink or chum salmon, due to extensive digestion (Table 2). One additional coho salmon had eaten two Pacific sandlance, *Ammodytes hexapterus*, but all other fish remains were too digested to positively identify. Out of the 23 tagged pink salmon found in the stomachs of these coho salmon, only 18 were sufficiently intact to permit measurements of their fork length (Table 2). The average length of these pink salmon was significantly less ($t = 8.02$; $P < 0.001$) than the average length of the pink salmon that were released (Fig. 2). Twelve of the eighteen tagged and measurable pink salmon found in the stomachs of the coho were clearly missing a pectoral fin. The pectoral fins of all the other fish were too digested to be certain whether or not they had been fin-clipped. The average length of the 12

TABLE 1.—Characteristics of tagged juvenile pink salmon released in each experiment and those subsequently recovered by beach seining. Nr = no. released; Ns = no. fish in prerelease sample; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = mean fork length; C.I. = 95% confidence interval for $\bar{X}$; Nc = no. of tagged salmon recaptured by beach seining; H = no. hours after release of tagged fish.

	Tagged fish released							Tagged fish recaptured						
Date	Species	Nr	Ns	Min	Max	$\bar{X}$	C.I.	Species	Nc	Min	Max	$\bar{X}$	C.I.	H
4/26/85	pink	3,000	99	34	41	38.1	37.9–38.4	pink	5	37	38	37.4	36.7–38.1	1.5
6/6/85	pink	1,800	100	36	51	44.4	43.8–44.9	pink	3	42	46	44.3	39.2–49.5	1–3
								pink	12	40	50	44.7	42.7–46.6	3–5
								pink	4	40	47	42.8	38.0–47.5	5–7
								pink	0	—	—	—	—	21–26

TABLE 2.—Number and size of juvenile salmon found in stomachs of predators in each experiment. Sets = no. beach seine samples; S = no. of stomachs examined; N = total no. juvenile salmon in stomachs; Nc = no. of tagged fish in stomachs; Nm = no. of tagged fish whose fork length could be measured; Min = minimum fork length; Max = maximum fork length; $\bar{X}$ = average fork length; C.I. = 95% confidence interval for $\bar{X}$; JS = juvenile pink or chum salmon.

					Juvenile salmon found in predator stomachs							
					All salmon		Tagged salmon only					
Experiment	Date	No. sets	Predator	S	Species	N	Nc	Nm	Min	Max	$\bar{X}$	C.I.
1	4/26/85	1	coho	210	pink	51	23	18	34	38	35.6	35.0–36.2
					chum	1	0					
					JS	14	0					
2	6/6/85	16	coho	374	pink	17	15	15	36	45	40.7	39.3–42.1
			staghorn	24	pink	0						
			Dolly Varden	15	pink	0						

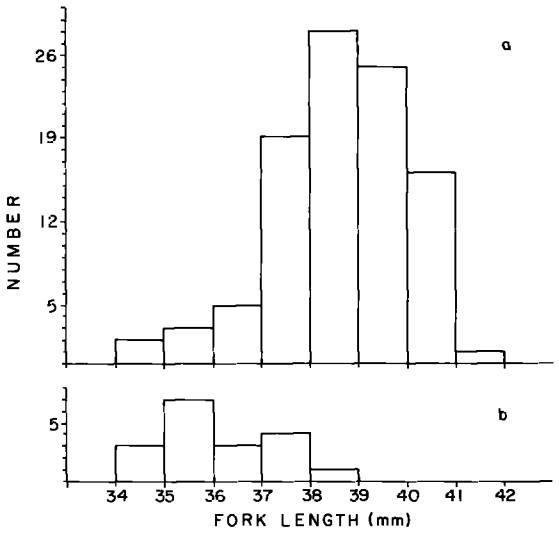

FIGURE 2.—Size-frequency distribution of sample of tagged pink salmon released in the first experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

fin-clipped fish was 35.4 mm, which is not significantly different ($t = 0.47$; $P > 0.50$) from the average length of the 18 tagged and measurable pink salmon.

Pink salmon released in the second experiment ranged in size from 36 to 51 mm fork length, with an average of 44.4 mm (Table 1). A total of 1 juvenile sockeye salmon, 1 juvenile chum salmon, 28 yearling coho salmon, 6 Pacific staghorn sculpin (*Leptocottus armatus*), 10 Pacific herring (*Clupea harengus pallasi*), approximately 500 larval walleye pollack (*Theragra chalcogramma*), 20 Pacific snake prickleback (*Lumpenus sagitta*), 1 red Irish lord (*Hemilepidotus hemilepidotus*), 6 Dolly Varden (*Salvelinus malma*), and 10 starry flounder were captured in the 2 beach seine sets done before the release. Examination of the stomach contents of all the coho salmon, five staghorn sculpins, the red Irish lord, and all the Dolly Varden provided no indication that any of these fish had recently eaten juvenile pink or chum salmon. The seven additional beach seine sets done on 6 June after the release of the tagged pink salmon captured a total of 271 coho salmon, 33 Dolly Varden, 46 staghorn sculpin, 2 coastal cutthroat trout (*Salmo clarki clarki*), 55 pink salmon, and 3 chum salmon. Nineteen pink salmon had been tagged (Table 1). All the untagged pinks were larger.

The stomach contents of 246 coho salmon, 14 Dolly Varden, and 16 sculpins were examined. There was no evidence that any of the Dolly Varden or sculpins had eaten any juvenile pink or chum salmon, although one sculpin had eaten a juvenile coho salmon. However, 13 of the coho salmon had eaten a total of 17 juvenile pink salmon, of which 15 had been tagged. The head was missing from one of the two untagged pink salmon so it could not be measured, but the fork length of the other was 51 mm. The tagged pink salmon found in the stomachs of the coho salmon were typically the smaller ones (Fig. 3), with an average length significantly less ($t = 5.06$; $P < 0.001$) than the average length of all pink salmon that were released in this experiment (Table 2).

No juvenile salmon were found in the stomachs of predators captured on 7 June. A total of 1 juvenile pink salmon, 141 yearling coho salmon, 1 Dolly Varden, and 115 staghorn sculpins were captured in 9 beach seine sets. The pink salmon was not tagged and none of these predators had recently eaten any juvenile pink or chum salmon. Five of the coho salmon had been branded, so the estimated total population of coho salmon in the vicinity of the release site was 4,047, with a 95% confidence inter-

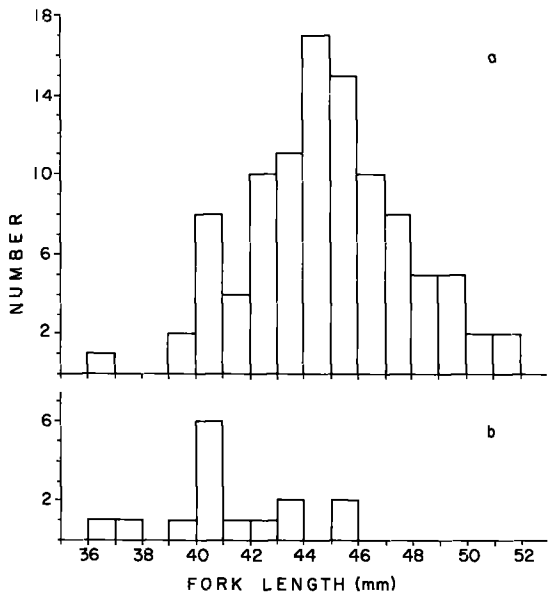

FIGURE 3.—Size-frequency distribution of sample of tagged pink salmon released in the second experiment (A) and all tagged pink salmon subsequently recovered from stomachs of predators (B).

val of 1,912 to 9,339. Based on these figures, it is estimated that coho salmon consumed a total of 162 (9%) of the tagged pink salmon released on 6 June, with a 95% confidence interval ranging from 76 (4%) to 375 (21%).

DISCUSSION

Determining the prey preference of predators in the wild is an important but difficult problem. The two experiments reported here illustrate a new approach to determining the selectivity of predators in the wild. Aside from logistic problems, the success of this method depends on the validity of four main assumptions: 1) predators that are captured and examined, and their stomach contents, are truly representative of the total predator population of interest; 2) tagging or marking the prey does not result in abnormal behavior of either the prey or predators; 3) ingestion and partial digestion of the prey by the predators does not significantly alter the characteristics of the prey that are of primary interest; 4) all of the tagged prey remain equally "available" to the predators for the duration of the experiment.

The first assumption should be valid if the sampling program is appropriately designed, considering the statistical tests that will be used to analyze the data. This is a complex topic and an in-depth discussion is beyond the scope of this paper. However, many extensive references are available (e.g., Anderson and McLean 1974; Cochran 1977; Montgomery 1976).

The two experiments reported here were designed only to demonstrate the utility of this approach and do not clearly show how generally applicable the results are. Only a small number of tagged fish were released and samples of predators were collected with a beach seine, which undoubtedly is biased to some degree in terms of the species and sizes of fish that were captured. In addition, the samples were collected at only one location in the first experiment and over a relatively small area in the second experiment. However, extensive sampling and examination of the stomach contents of fish predators over a 3-yr period indicates that yearling coho salmon are the major predators of juvenile pink salmon throughout Masset Inlet and Masset Sound (Hargreaves in press). The results of these two experiments are also consistent with those obtained from enclosure experiments, which indicate that yearling coho salmon are size selective when feeding on juvenile pink or chum salmon (Parker 1971; Hargreaves and LeBrasseur 1986). Thus, although quite limited in scope, these two experiments provided results that are consistent with those obtained by two other independent, but considerably more expensive and laborious, methods.

The assumption that tagging and marking the prey does not affect the behavior of predators or prey can be assessed either by direct observation or by conducting additional experiments. In some cases it may be possible to design the experiment to allow observation of both the predators and prey throughout the experiment and directly observe any unusual behavior. However, in many cases, additional experiments will probably be required. For the two experiments reported here, the pink salmon used in the first experiment were tagged and fin-clipped; the fish released in the second experiment were tagged but were not fin-clipped. The results of the first experiment indicate that tagging was more effective than fin-clipping for recognizing fish recovered from the stomachs of predators. In terms of behavioral changes, previous work indicated that the mortality of tagged and untagged juvenile salmon was not significantly different when exposed to predators and that tagging juvenile salmon had no noticeable affect on the behavior of either the predators or prey (Hargreaves and LeBrasseur 1986). However, the tagged fish used in these enclosure experiments were not fin-clipped.

Earlier studies have indicated that amputation of fins from juvenile salmon typically results in lower survival rates (Ricker 1949). Marked pink salmon fry also suffer higher mortality than unmarked fry, possibly due to a bias on the part of predators for marked prey (Parker et al. 1963). This is not a major concern in the two experiments reported here because the intent was to determine the size selectivity of predators, rather than any selectivity for marked or unmarked prey. In addition, fin-clipped pink salmon were used only in the first experiment but predators consumed significantly more of the smaller prey in both experiments. This supports the assertion that fin-clipping the pink salmon did not substantially affect the prey size selectivity of the predators. In general, the possibility that the results of these types of experiments may not apply to untagged or unmarked prey can be eliminated by using only tags or marks that are known to have negligible effects on the behavior of both the prey and predators.

The third assumption, that ingestion and partial digestion of the prey by the predators does not significantly alter the important characteristics of the

prey, can often be directly verified. For the two experiments reported here, prey size (fork length) was the characteristic that was most important. The observed difference between the average length of the tagged prey that were released and the tagged prey subsequently recovered from the stomachs of predators was 2.5 mm (6.6%) in the first experiment, and 3.7 mm (8.3%) in the second experiment. These are small differences, and the possibility that they might be due to experimental error rather than predator selectivity must be considered. All length measurements were made to the nearest millimeter and numerous remeasurements indicated that measurement errors were negligible at this level of accuracy. To eliminate the possibility that the length of the tagged fish might decrease if they were preserved (Parker 1963), live fish were used to determine the length-frequency distribution of the prey prior to release and all prey recovered from the stomachs of predators were immediately measured. Burgner (1962) reported that the length of sockeye salmon smolts decreased by 2–3% because of *rigor mortis* alone. However, experiments conducted in Masset Inlet in 1984 indicated much smaller changes occur after death in juvenile pink salmon. At temperatures of 9°–10°C, the average length of 26 juvenile pink salmon of known length, fed to and subsequently recovered from the stomachs of 19 yearling coho salmon, decreased less than 1% for periods of up to four hours after ingestion (Hargreaves unpubl. data). In the two experiments reported here, numerous beach seine sets were made to capture potential predators, but all of the tagged pink salmon found in their stomachs were recovered within four hours of the releases of tagged prey. Shrinkage of the prey after ingestion therefore can account for only a small portion of the observed differences in size between the prey that were released and those that were found in the stomachs of predators.

The fourth assumption, that all tagged or marked prey remain equally "available" to predators throughout the experiment, will usually prove to be the most difficult to assess and verify. The availability of prey to predators frequently depends on characteristics of the predators (hunger level, visual acuity, mobility, body or gape size, individual or group behavior, etc.), the prey (abundance, coloration, size, speed, endurance, behavior, etc.), and the environment (habitat complexity, light conditions, etc.). These parameters can interact in a complex manner, so that it is typically only in the simplest situations that all factors that affect the availability of prey to a predator can be thoroughly investigated and understood (Curio 1976; Zaret 1980).

Predators consumed significantly more of the smaller prey in both experiments reported here, despite substantial differences in the physical characteristics of the two release sites, time of year, and various characteristics of the predators (abundance, species composition, size, feeding history, etc.). This suggests that the availability of prey to the predators was not substantially affected by variations in the characteristics of either the predators or the environment. It also appears reasonable to assume that prey of all sizes remained equally available to predators during both experiments. All of the tagged prey were one species and received identical treatment prior to release. There is no reason to think there were any substantial differences in the physical characteristics among the prey at the time of release, aside from the desired variation in size.

It is conceivable, however, that differences in prey behavior or size might have indirectly influenced the availability of prey to the predators. For example, extensive sampling of juvenile salmon in Masset Inlet has indicated a tendency for larger pink salmon to be concentrated further offshore than smaller pink salmon during the early sea-life period (Hargreaves et al. 1987a, b). Swimming speeds of salmon are also known to increase rapidly with increasing body size (Brett 1965). Thus, if there was any tendency for tagged salmon to rapidly swim away from the release sites, larger fish may have left quicker than smaller fish. The result could be a decrease in the average size of tagged salmon found in the immediate vicinity of the release site and the incorrect conclusion that predators were selectively feeding on the smaller prey.

In fact, however, this possibility appears unlikely. In both experiments the size of the live, tagged fish recovered along with the predators was not significantly different than the size of the fish that had been released as much as nine hours earlier (Table 1). There is also no indication that the mean size of these fish changed in a consistent manner over the course of the second experiment. These results suggest that, if there was any segregation of tagged prey after release, it was probably minor and did not appreciably affect the availability of prey to the predators.

In general, complications arising from variations in the availability of prey to the predators may be reduced or eliminated by limiting the duration of the experiment. If all of the prey are released at one time and location, it is reasonable, and in most cases

probably valid, to assume that all prey are equally available to any predators captured in the immediate vicinity a short time later. The amount of time during which the prey subsequently remain equally available to predators will likely vary from one situation to the next. If the prey are very mobile, probably some will eventually become less or more accessible to predators than others. This possibility can be eliminated or at least minimized by keeping the experiment short enough to ensure that the prey do not have sufficient time to segregate or move away from the release site. The magnitude of this problem and thus the appropriate duration for each experiment may be assessed by recapturing some of the tagged prey after the release. The experiment should be terminated when the characteristics of the recaptured prey begin to diverge significantly from those of the original prey population.

Determining the prey preference of predators in the wild is a concern to many biologists. All methods of determining the prey selectivity of predators in the wild are, and will likely continue to be, hampered by the complexity of the related problem of determining the relative "availability" of prey to predators. The advantage of the method proposed here is that it allows the investigator to control some of the major variables that are known to affect the availability of prey. The most important characteristics of the prey (species ratios, abundance, size ranges, etc.) can be determined before any predation occurs and in many cases can also be precisely controlled. The predators remain free to feed on all types of prey in the study area, but for the purposes of the investigator, the choice of prey can effectively be reduced to those with known characteristics and origin. This is a major advantage when compared with the more traditional approach of calculating selectivity indices, as it eliminates the need to determine the relative abundances of prey in the field. It also substantially reduces the ambiguity associated with interpreting selectivity indices for highly mobile predators, where typically there is little or no information available concerning the area traveled by the predator during the feeding period and thus what prey were actually available to the predator.

The specific goal of the two experiments reported here was to determine if predators were size selective when preying on juvenile pink salmon during the early sea-life period. The results indicate that yearling coho salmon were the dominant predator of juvenile pink salmon at two locations, one in Masset Inlet and the other in Masset Sound, and that the average size of juvenile pink salmon consumed by these predators was significantly less than the average size of pink salmon that were released. These results are consistent with those obtained from two other independent approaches and suggest this method may be a viable and cost-effective alternative for determining the prey preferences of predators in the wild. It may be particularly useful for assessing prey preferences of predators feeding on juvenile salmon near hatchery facilities in Canada and the United States, where millions of juvenile salmon are currently tagged and released each year.

ACKNOWLEDGMENTS

Suggestions and comments from an anonymous reviewer are greatly appreciated. Robin LeBrasseur and Owen Kennedy assisted with the supervision of the field experiments and analyses of the stomach samples. Bruce Patten, Lui Marinelli, Tom Poole, Josette Weir, Rick Hobbs, Ted Carter, and Bob Hungar helped to capture, tag, and sort the juvenile salmon and assisted in the beach seining and processing of samples collected in the various experiments. Trans-Provincial Airlines generously permitted unlimited use of their seaplane wharf and other facilities at Masset, B.C. to conduct the second experiment during 6 and 7 June 1985.

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EXPERIMENTAL MANIPULATION OF POPULATION DENSITY AND ITS EFFECTS ON GROWTH AND MORTALITY OF JUVENILE WESTERN ROCK LOBSTERS, *PANULIRUS CYGNUS* GEORGE

RICHARD F. FORD,[1] BRUCE F. PHILLIPS,[2] AND LINDSAY M. JOLL[3]

ABSTRACT

A density manipulation experiment was conducted at Seven Mile Beach, Western Australia, to compare growth and mortality for different density groups of juvenile western rock (spiny) lobsters, *Panulirus cygnus*, inhabiting limestone patch-reefs. Juveniles on a control reef were left at their natural, high densities while those on a treatment reef were reduced to approximately 25% of the original, natural density by trapping and reintroduction, which maintained the original size-frequency distribution. Mark-recapture studies were conducted on each reef at three monthly intervals for a year to estimate size-specific growth rates, population densities, and mortality rates. Direct counts of individuals were made by divers to estimate total numbers of juveniles on each reef. There were no statistically significant differences in growth rates for any age category between the control and treatment reefs, but there were significant differences in size-specific mortality rates between the treatment and control groups, with much lower mortality on the treatment reef. Our results suggest that markedly reduced densities of juveniles on a reef may lead to a corresponding reduction in mortality, but no effect on growth was evident. However, part of the apparently higher mortality on the control reefs may instead have been due to emigration of tagged individuals to other reefs. The difficulties of conducting manipulation experiments in the field on a highly mobile species are discussed.

The western rock (spiny) lobster, *Panulirus cygnus*, occurs on the coast of Western Australia from North West Cape (lat. 22°S) to Cape Naturaliste (lat. 34°S). Juveniles (2–5 years old) inhabit the coastal limestone reefs, primarily at depths of 1–10 m (Chittleborough and Phillips 1975). They remain on the reefs for several years, apparently with little movement from one area to another (Chittleborough 1974a). Joll and Phillips (1984) found that the juveniles feed on a variety of animals and plants associated with the seagrass beds surrounding the reefs. Following the spring molt, larger animals (ages 4–6) move to the adult habitats in depths of 30–150 m (Morgan et al. 1982).

Chittleborough (1970) observed that, near the center of the geographical range, recruitment of small juveniles appeared to exceed the holding capacity of the reef system. He concluded that density-dependent mortality of the juveniles at such sites limits their recruitment to the adult stock. He also observed reduced growth rates of animals at these sites and considered that the available food resources may be inadequate for the maintenance of optimum growth at such high densities.

Although there have been many field studies on the ecology of spiny lobsters (see review by Kanciruk 1980), none have attempted experimental manipulation to elucidate the effects of population density on growth and survival. This paper considers the growth and survival of juvenile *P. cygnus* inhabiting experimental and control patch-reefs at Seven Mile Beach, following a manipulation designed to reduce the density of juveniles of the experimental reef. The hypothesis to be tested was that high population densities of juvenile lobsters limit the growth and survival of the western rock lobsters. Despite its inherent practical problems, a manipulation approach was adopted as the one most likely to yield direct evidence to evaluate the hypothesis.

Manipulation experiments are best done using replicated experimental areas and both increases and decreases in the density of the species under consideration (Connell 1974; Underwood 1979). However, where species (such as lobsters) cannot be transplanted or enclosed effectively, the only practical option is to simply reduce densities (Connell 1983). In the case of the study described here, there are also practical limitations in finding sufficiently

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similar experimental areas to employ as replicates and in selecting control reefs which are equivalent to the premanipulation condition of experimental reefs. In this experiment juveniles on one reef, selected as the control site, were left at natural, high densities, while those on another, selected as the treatment site, were reduced to approximately 25% of their original, natural density. A third reef, also left at its natural high density, was monitored at a lower level to examine the degree of representativeness of the control.

METHODS

Reef Study Sites

Three limestone patch-reefs at Seven Mile Beach, Western Australia (lat. 29°08'S; long. 114°54'E), designated as reefs I, III, and V (Fig. 1), were used as the study sites. These three test reefs are typical of those at Seven Mile Beach in terms of both their structure and biota. Observations by divers also indicated that the size structure of *P. cygnus* on each reef was similar. The patch-reefs occupy a lagoon environment between the beach and a limestone barrier reef approximately 400 m offshore. Each patch-reef is surrounded by a calcareous, sandy substrate and areas of limestone, which both support extensive seagrass beds of mixed species composition, the primary feeding areas for juvenile *P. cygnus* (Cobb 1981; Joll and Phillips 1984). Seagrass species of the genera *Amphibolis*, *Heterozostera*, and *Halophila* dominate in these beds. The reefs themselves are covered by *Amphibolis* spp. and by a variety of algal species.

The approximate area of reef III, the treatment reef, is 0.104 ha, and that of reef V, the main control reef, is 0.103 ha. Reef I, the secondary control reef, has an area of approximately 0.071 ha. Reef I is located approximately 750 m south of reef V, while reef III is located approximately 60 m directly west and offshore from reef V (Fig. 1). Adequate separation of the treatment and control reefs from each other for the purposes of the experiment was assumed, based on maximum foraging ranges of up to 50 m for *P. cygnus* in the Seven Mile Beach area reported by Chittleborough (1974a). Water depths are 2–3 m around reefs I and V and 3–5 m around reef III. The tops of the reefs are nearly exposed at low tide.

Single Molt Increments, Annual and Seasonal Growth

The numbers of juvenile *P. cygnus* from each reef which were sexed, measured, and marked or re-

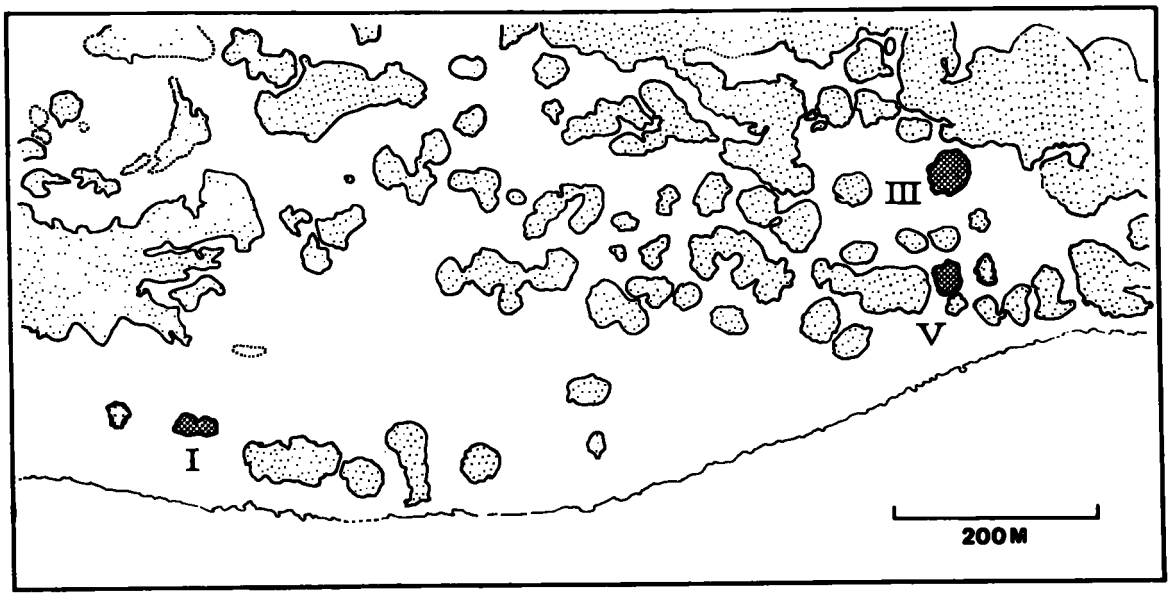

FIGURE 1.—Map of study area at Seven Mile Beach, Western Australia, showing the locations of reefs, I, III, and V (dark shaded) in relation to other reefs (light shaded).

moved in January 1981 at Seven Mile Beach are given in Table 1. Animals with carapace lengths (CL) ≥40 mm were marked with individually numbered western rock lobster tags (Chittleborough 1974b). Animals with CL <40 mm were marked with individually numbered Floy[4] No. FD-68B spaghetti tags (Davis 1978). Growth data were obtained from tagged individuals recaptured on the three test reefs during resampling in February, March, May, August, and September 1981, and January and February 1982. Growth of tagged *P. cygnus* between recaptures over the period January to May was used to provide data on single molt increments.

Size and Age Structure

Age classes were identified from length-frequency distributions, as described by Chittleborough (1970) and Chittleborough and Phillips (1975). From analysis of the size structure present in January 1981, juveniles up to 38.0 mm CL were judged to be 2 years of age at that time; 38.1–55.0 mm, 3 years of age; 55.1–68.0 mm, 4 years of age; and those >68.1 to be 5 years of age or older. Similarly for January 1982, animals up to 42.5 mm CL were considered to be 2 years of age at that time; 42.6 mm–55.0 mm, 3 years of age; those 55.1–68.0 mm to be 4 years of age; and those >68.1 to be 5 years of age or older.

Population Size, Density, and Mortality Rates

Estimates of the population size, density, and mortality rates of *P. cygnus* juveniles on reef I have been made at Seven Mile Beach since 1970, using recaptures from baited traps (Chittleborough 1970; Chittleborough and Phillips 1975). These estimates for reef I were continued during the period of this study on reef I and, in addition, estimates were also undertaken for reefs III and V, using the same traps and mark-recapture methods. In the present study, 12–13 traps were set around the perimeter of each test reef to ensure catches directly from the area of the reef. At each sampling time an array of 12–13 traps was set simultaneously around reefs III and V in an attempt to reduce attraction by traps of *P. cygnus* from one reef to another.

During the initial tagging in January 1981, trapping was conducted on each reef for four consecutive days, while during each subsequent recapture

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

TABLE 1.—Numbers of juvenile *Panulirus cygnus* examined on three reefs at Seven Mile Beach, Western Australia.

	Sampling dates							
Reef	1981	1981	1981	1981	1981	1981	1982	1982
	9–10 Jan.	6–7 Feb.	Mar.	May	26–27 Aug.	21–22 Sept.	26–27 Jan.	26–27 Feb.
Reef I								
No. caught	463	447	—	—	362	300	498	419
No. tagged	463	—	—	—	—	—	—	—
No. recaptured	—	103	—	—	98	72	88	[1]5
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef III								
No. caught	1,202	785	475	233	221	359	791	862
No. tagged	304	—	—	—	—	—	—	—
No. removed from reef	898	306	150	—	—	—	—	—
No. recaptured	—	[2]+	+	54	52	55	204	[1]13
	11–15 Jan.	4–7 Feb.	10–11 Mar.	5 May	24–25 Aug.	19–20 Sept.	24–25 Jan.	23–25 Feb.
Reef V								
No. caught	141	682	596	424	599	631	703	696
No. tagged	1,141	—	—	—	—	—	—	—
No. recaptured	—	278	214	154	212	285	140	28

[1]Additional to those recaptured in January 1982.
[2]+ = not scored.

period trapping was conducted for two consecutive days. The single mark-recapture estimate of Bailey (1951) was used to calculate population sizes.

Visual Estimates of Population Size

Direct estimates of the total number of juveniles present on each test reef were made by two divers during the day. Initially the surface of each test reef was mapped, and the map was transferred to acetate writing sheets for use underwater, so that major features such as crevices, holes, and sections of ledges could be recognized and searched in a uniform manner during each census. The two divers moved slowly around and over the reef, counting and recording juvenile *P. cygnus*. Underwater lights were used to aid in this process. Repeated counts were often necessary to obtain consistent results for sections of the reef with large aggregations of juveniles. One diver followed approximately 2–3 m behind the other, and after each section of the reef was censused, the numbers of juvenile *P. cygnus* recorded by the two divers were compared. Only three observers conducted all of the visual censuses and, after experience was gained initially, differences between total counts by any two divers on a reef usually were less than 5%. Counts by the two divers were compared for 12 of these censuses, employing separate Wilcoxon signed-rank tests in which the data recorded by each diver for a given section of the reef were paired. The results for all 12 censuses indicated no significant differences in counts between divers ($P > 0.05$).

There are two primary sources of error in this method. One is that few individuals <40 mm CL can be seen on the surface of the reef or in holes or crevices. The other results from reduced visibility caused by turbidity and water turbulence. This second problem was largely avoided by only doing counts when conditions of turbidity and water turbulence were favorable.

During January–June 1981 and October 1981–February 1982, visual density estimates were obtained monthly or bimonthly in reefs III and V. However, storm conditions and poor visibility during the remainder of 1981 precluded observations. Visual density estimates were conducted on reef I during January 1981 and in January and February 1982, while in January and February 1983 estimates were conducted on all three test reefs.

Density Manipulation Experiment

All of the juvenile *P. cygnus* caught on reefs I and V (the control reefs) in January 1981 were tagged, measured, and released. On reef III (the treatment reef) 1,202 *P. cygnus* were caught during four consecutive days in January 1981 and graded into size categories (5 mm CL size intervals). This was done by measuring the animals and holding them in water in mesh bags suspended from the side of the boat during the 2–3 hours required for processing.

To reduce the population of lobsters on reef III by approximately 75%, three out of each four animals in each size group were removed from the reef and translocated to another locality out of the Seven Mile Beach area. Selection was done by removing the appropriate number of individuals from each size category blindly to avoid bias. This helped to assure that the groups of juveniles returned to reef III had a size frequency and sex ratio similar to those of the original population. The remaining 304 juveniles caught from reef III were remeasured, tagged, and released on that reef. During the next two sampling periods in February and March 1981, any untagged *P. cygnus* caught on reef III were removed (Table 1) to aid in maintaining the density at approximately 25% of its natural level.

Analysis of the Growth Data

Two types of growth data were examined: 1) the single molt increments of animals with <4 legs missing (based on the growth of animals recaptured within four months of a previous capture) (Chittleborough 1976), and 2) the average relative growth rate (Sandland and McGilchrist 1979), which has been shown to be appropriate for analyses of *P. cygnus* growth (Phillips et al. 1983). The data were classified by reef, sex, age class, duration, and time of year at liberty and by the number of legs missing at the time of tagging.

The average relative growth rate data of *P. cygnus* were condensed into a three-factor nonorthogonal experimental design with missing cells. The data were analyzed by examining differences in growth between test reefs for each age and recapture interval, using the Wilcoxon rank sum test, and by examining age, recapture interval effects, and their interaction in a two-factor nonorthogonal analysis of variance.

In addition to *P. cygnus* caught on the reef of original tagging, 75 individuals (12%) were recaptured on both reefs III and V. The data for the 49

of these which showed growth between tagging and recapture were initially analyzed separately.

Chittleborough (1970) found that loss of more than three legs depressed growth. This was confirmed for our data by an analysis comparing the average relative growth rates of *P. cygnus* in the two leg-loss classes (<3 legs missing and ≥4 legs missing), using a *t*-test. There was a significant difference in growth rates between the two leg-loss classes ($P > 0.05$). Although this difference is confounded with differences in the other factors, the result was considered as sufficient evidence, when combined with Chittleborough's findings, to exclude from further analysis data for *P. cygnus* with ≥4 legs missing.

A further analysis was performed to determine if the growth rates of males and females differed. These analyses were done separately for each reef, age class, and recapture interval, using the Wilcoxon rank sum test. The results revealed no significant differences in average relative growth rates between the sexes ($P > 0.05$), so the data for males and females of the same age group were pooled.

RESULTS

Of the 304 tagged *P. cygnus* on reef III, 186 (61.2%; 87 males and 99 females) were never recaptured, while of the 1,141 animals tagged on reef V, 636 (55.7%; 324 males and 312 females) were never recaptured. Similarly, of the 463 *P. cygnus* tagged in January 1981 on reef I, 307 (66.3%; 162 males and 145 females) were never recaptured. Comparison of the size ranges and size-frequency distributions of *P. cygnus* tagged on the three reefs in January 1981 with those not recaptured (Fig. 2) indicated that the "losses" were distributed equally over the full size range and therefore may be assumed to be random. Ratios of males and females in these "losses" did not differ significantly from the male:female ratios in the original tagged population (chi-square test of independence, $P > 0.05$).

None of the tagged *P. cygnus* on reef I were recaptured on reef III or V. However, 75 (12%) of the tagged *P. cygnus* either on reef III or V were subsequently recaptured on the other reef, and some were caught several times on reefs III and V. However, only four of the animals originally tagged on reef III were ever recaptured on reef V, suggesting a general movement of *P. cygnus* from reef V to reef III, i.e., inshore to offshore.

Size and Age Structure

The size-frequency distributions of *P. cygnus* juveniles on reef I in January 1981 and January 1982 and that of the juveniles recaptured in January 1982 are shown in Figure 3. Similarly, the size-frequency distributions of juveniles on reefs III and V in January, May, and September 1981 and in January 1982 are shown in Figure 4. There was change in the composition of the population on reef I between January 1981 and 1982, indicating immigration of 2- and 3-yr-old animals into the population of this reef. Between January and September 1981 there was an indication of immigration of untagged animals to both reefs III and V, principally of animals ≥3 years of age, while in January 1982 there was also an obvious immigration of 2-yr-old animals to both reefs.

Population Size, Density, and Mortality Rates

The estimates of population size, density, and mortality rates for *P. cygnus* juveniles ≥3 years of age on reefs I, III, and V are given in Table 2. The estimate made for the population on reef III in February 1981 assumes that the 304 tagged *P. cygnus* released in January were still within the population in February.

The population densities of ≥3-yr-old juveniles on reef I estimated each January from 1970 to 1982 are shown in Figure 5. The density in January 1981, at the time the study began, was the highest ever recorded. The density in January 1982 was also very high and only exceeded by the levels in January 1974 and January 1981.

The annual mortality coefficient for juveniles aged

TABLE 2.—Population size, population density and mortality-rate estimates for juvenile *Panulirus cygnus* >3 years of age on three test reefs at Seven Mile Beach, Western Australia.

	[1]Reef 1 (0.071 ha)		[2]Reef III (0.104 ha)		[3]Reef V (0.103 ha)	
Date	Population	SD	Population	SD	Population	SD
Jan. 1981	1,990	170	2,192	194	2,644	120
Feb. 1981	—	—	1,879	195	—	—
Aug. 1981	625	38	725	54	1,042	40
Jan. 1982	1,273	93	1,951	92	1,841	101

[1]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.655.
[2]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.302.
[3]Annual instantaneous mortality coefficient for those >3 years in 1981 = 1.825.

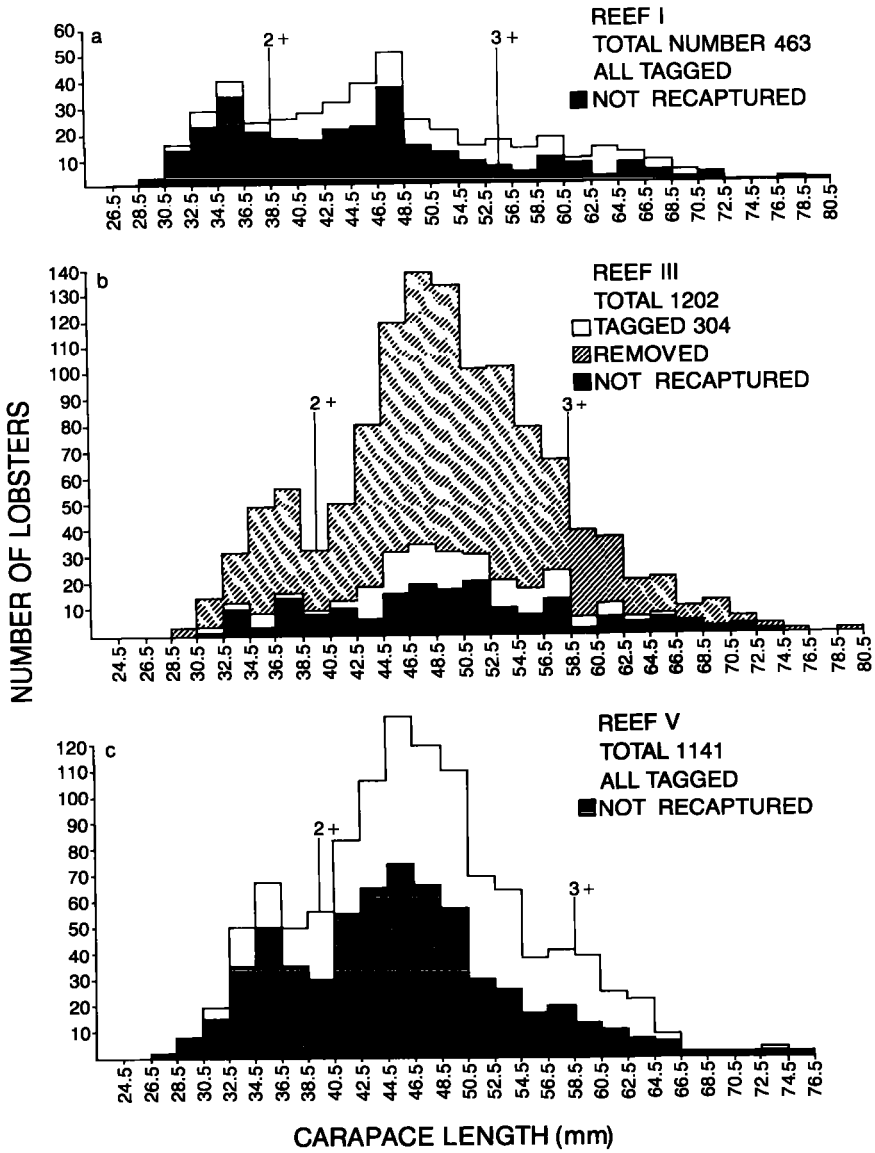

FIGURE 2.—Size-frequency distributions of juvenile *Panulirus cygnus* in January 1981 on three test reefs (reefs I, III, and V) at Seven Mile Beach, Western Australia and size-frequency distributions of animals removed or tagged. Size-frequency distributions of tagged animals not subsequently recaptured also are indicated.

≥3 years on reef III was slightly lower than that for juveniles on reefs I and V. Comparison of the estimates of population size on which these mortality coefficients were based showed that annual survival of animals ≥3 years old was significantly higher on reef III than on reef V (chi-square test of independence, $P < 0.005$).

The numbers of juveniles tagged and released on each test reef in January 1981 are shown in Table 1, while the numbers and percentages of those same individuals recaptured on the same reef in January or February 1982 are summarized in Table 3 for each age group. These data were used, in part, to provide more specific estimates of age-specific sur-

vivorship over the 1-yr period, based on assumptions considered later in this paper. A striking feature of the data for reef III is the very high percentage of recaptures, ranging from 97.4 to 100% for 3-, 4-, and ⩾5-yr-old individuals, and with a somewhat lower value of 58.1% for 3-yr-old animals. Percentage recaptures for all age groups combined were 71.4% on reef III, as compared with much lower values on reef V (14.7%) and reef I (20.1%). Separate comparisons employing chi-square tests of independence indicated that the number of juveniles recaptured were significantly higher on reef III than on reef V for each of the four age groups ($P < 0.005$).

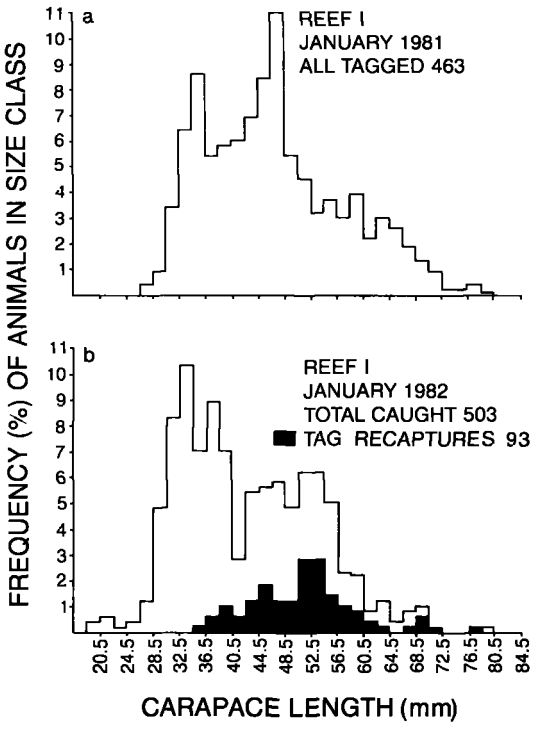

FIGURE 3.—Size-frequency distributions of juvenile *Panulirus cygnus* on Reef I at Seven Mile Beach, Western Australia, in January 1981 and 1983.

Visual Estimates of Population Size

Estimates of the mean total numbers of *P. cygnus* juveniles on the three test reefs, based on visual sampling by two divers, are summarized in Table 4.

The data for reef I are incomplete but show a dramatic decrease from 265 on 10 January 1981 to 66 on 19 January 1981. There was also an overall reduction from 265 in January 1981 to 181 in January 1982 and 173 in January 1983.

The data for reef III (Table 4) indicate that removal of *P. cygnus* by trapping on 11–15 January 1981 reduced the number of juveniles from 705 present on 10 January to about half of that number, with 395 (56%) observed on 19 January and 346 (49%) on 3 February. Further removal by trapping on 4 and 5 February 1981 reduced the number of juveniles to approximately 29% of the original 10 January level (205 observed on 18 February).

From March through June 1981 the mean estimated numbers of juveniles on reef III varied from 189 to 260, representing approximately 27–48 ($\bar{x}$ = 36%) of the original, natural population level observed on 10 January 1981 (Table 4). By January 1982, the number of juveniles on reef III had increased to 430, or approximately 61% of the level observed in January 1981 and by January 1983 the number had increased to 590 or approximately 84% of the natural level two years before.

The numbers of juveniles on reef V were rather more variable, ranging from a low of 72 (25 March 1981) to a high of 780 (October 1981). Of special im-

TABLE 3.—Number and percentage of juvenile *Panulirus cygnus* tagged in each age class on three reefs at Seven Mile Beach, Western Australia, in January 1981, and the numbers present and recaptured in January and February 1982.

	Reef I				Reef III				Reef V			
Age class (Yr)	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%	1981 No. tagged	1982 Total no. caught	1981 Recaptures No.	%
2	117	260	12	10.3	38	227	37	97.4	192	338	12	6.3
3	245	196	62	24.4	203	375	118	58.1	777	267	102	13.1
4	77	36	14	18.2	57	109	56	98.2	149	112	45	30.2
⩾5	15	6	5	33.3	6	92	6	100.0	23	14	9	39.1
Total	463	503	93	20.1	304	804	217	71.4	1,141	731	168	14.7

[1]In January 1981

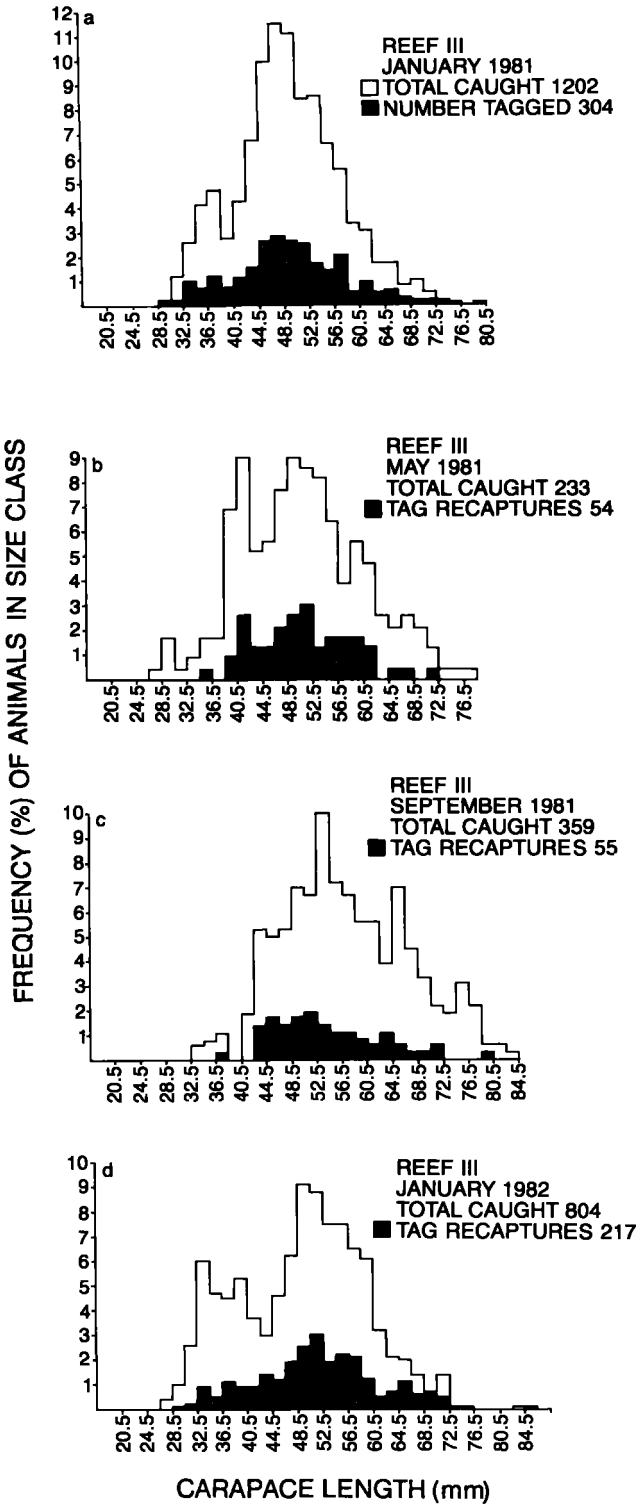

FIGURE 4.—Size-frequency distributions of juvenile *Panulirus cygnus* on reefs III and V at Seven Mile

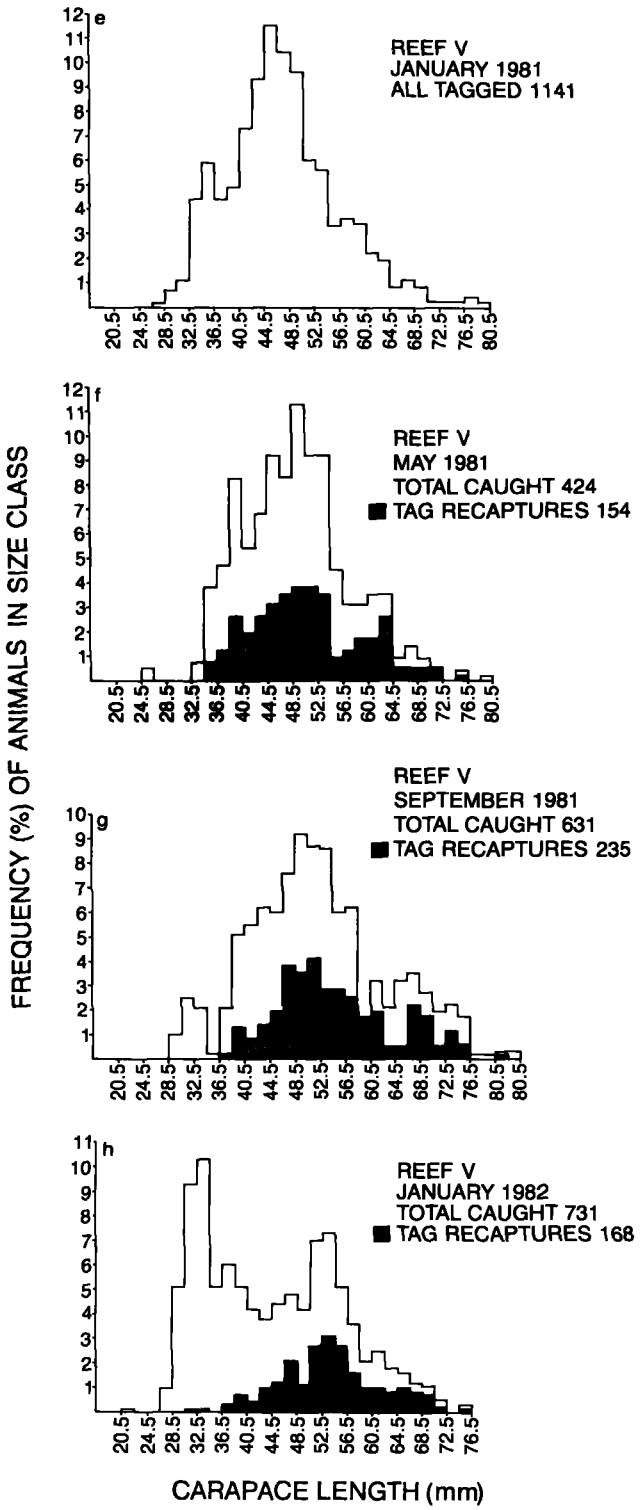

FIGURE 4.—*Continued*—Beach, Western Australia, during the period January 1981 through January 1982.

portance was the 34% decline in numbers between 10 January and 18 February on reef V. By mid-February 1981 the estimated population on reef V was below that on reef III. The mean number of animals for reef V in February 1982 (401) was 71% of that observed in January 1981 (563), although in October, November, and December 1981 it exceeded the January 1981 level. In January 1983, the number of juveniles (537) was essentially the same as that observed two years before (Table 4).

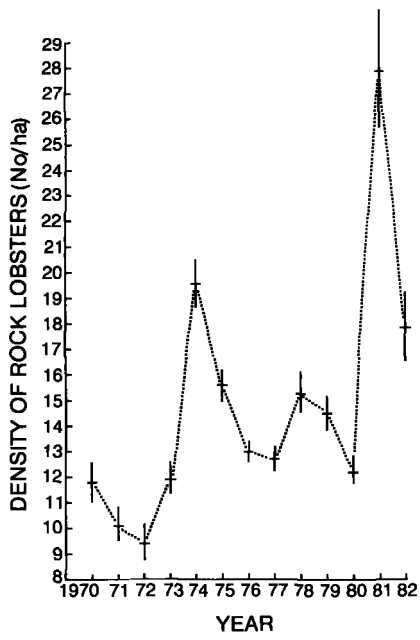

FIGURE 5.—Densities of 3-yr-old juvenile *Panulirus cygnus* in January on reef I at Seven Mile Beach, Western Australia, for the period 1970 through 1982. Mean and 95% confidence limits are shown. Data for 1970–80 from Morgan et al. (1982).

TABLE 4.—Mean total numbers of juvenile *Panulirus cygnus* on three test reefs at Seven Mile Beach, Western Australia, based on visual estimates made by two observers. — = no visual estimate made.

Date	Reef I	Reef III	Reef V
10 January 1981	265	705	563
19 January 1981	66	395	286
3 February 1981	—	346	235
18 February 1981	—	205	191
9, 13 March 1981	—	335	227
25 March 1981	—	189	72
23 April 1981	—	233	220
15, 17 June 1981	—	260	451
15 October 1981	—	374	780
19 November 1981	—	424	680
10 December 1981	—	321	647
29 January 1982	181	430	—
23 February 1982	42	474	401
11 January 1983	173	590	537
16 February 1983	121	521	501

Growth

Single Molt Increments

Mean single molt increments of male and female *P. cygnus* on reefs III and V, the treatment and control reefs, (Table 5) showed no significant difference within either the 2-, 3-, or 4-yr-old age-classes (t-test, $P > 0.05$). Only four animals estimated to be ⩾5 years of age were recaptured and these were all from reef V. After pooling the molt increment data for the two sexes there were no significant differences between the mean single molt increments of 2-, 3-, or 4-yr-old animals on reefs III and V (t-test, $P > 0.05$).

TABLE 5.—Mean molt increments in carapace length (mm) for sex age-class groups of juvenile *Panulirus cygnus* from three test reefs at Seven Mile Beach, Western Australia during January–May 1981. Data are mean SE (n).

Age class	Reef I		Reef III		Reef V	
	Males	Females	Males	Females	Males	Females
2	—	—	2.58(0.40) (5)	1.84(0.11) (5)	1.75(0.28) (4)	2.41(0.20) (10)
3	2.85(0.56) (6)	1.74(0.21) (9)	2.01(0.33) (16)	1.76(0.15) (16)	2.27(0.14) (76)	2.17(0.26) (60)
4	—	—	2.75(0.61) (4)	1.94(0.26) (5)	3.17(0.26) (16)	2.88(0.19) (18)

The data from reef I, the secondary control reef, were only sufficient for an examination of the single molt increments of 3-yr-olds. Within this age class there was no significant difference in mean molt increment between the two sexes and the data for the whole age class were pooled. There were no significant differences between the mean single molt increment for 3-yr-olds from reef I and the mean single molt increment for this age class on either reefs III or V (t-test, $P > 0.05$).

Annual and Seasonal Growth

The mark-recapture data from reefs I, III, and V are considered within four time periods: From January 1981 to May 1981 (the "summer–autumn" period), from May 1981 to September 1981 (the "winter" period), from September 1981 to February 1982 (the "spring–summer" period) and from January 1981 to January–February 1982 (the "annual" growth period). As described in Methods section above, average relative growth rates (ARGRs) of males and females were not significantly different and therefore the data were pooled. Because of the small number of ≥5-yr-old lobsters, their growth data were combined with the data for the 4-yr-old individuals. The ARGRs of the different age groups from all three reefs over each of the four time periods are given in Figure 6.

Comparison of growth data for the test reefs for each age group and recapture interval were made using Wilcoxon rank sum tests. The primary purpose was to evaluate whether growth data for the three reefs could be pooled for later analysis. The comparisons are of interest in their own right, but caution is required in interpreting some of the differences established because of small sample sizes in some cells.

The results showed no significant differences in ARGRs of any age group between reefs III and V ($P > 0.05$), the treatment and the principal control reefs respectively in the density manipulation experiment. There were significant differences in ARGRs between reefs I and III for individuals 3 years of age in January–May 1981, May–September 1981, and January 1981–January 1982 and for individuals ≥4 years of age in January–May 1981. There also were significant differences in ARGRs between reefs I and V for individuals 3 years of age in January–May 1981 and May–September 1981, and for individuals ≥4 years of age in January–May 1981 ($P < 0.05$). The significant differences all showed consistently higher ARGRs on reef I than on reefs III and V.

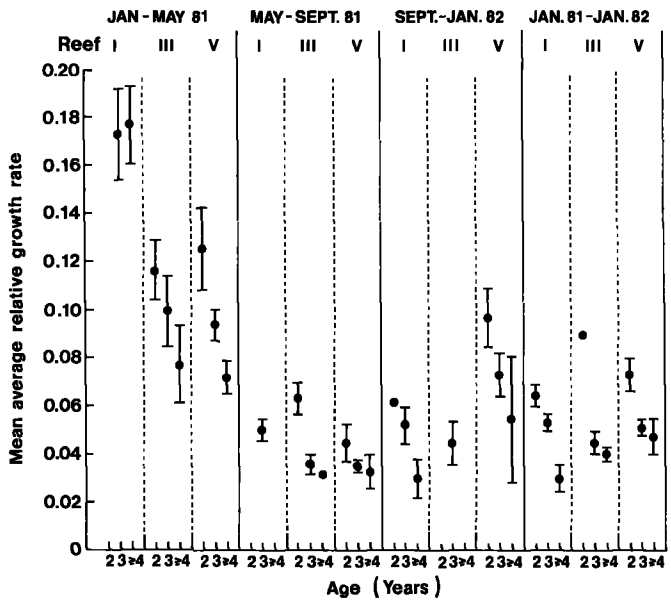

FIGURE 6.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs at Seven Mile Beach, Western Australia.

The data for both reefs III and V were then pooled. The data for 49 *P. cygnus* which were recaptured on reefs III and V were included in this set (Fig. 7). Comparisons of these combined data were made with the data for reef I, and the results indicate that all of the significant differences in growth described above were maintained except that for 3-yr-old individuals in January 1981–January 1982. The lack of a consistent significant difference between reefs at all ages and recapture intervals suggests that the effect is not a simple response to a superior environment, but rather that interactions between reef and age and between reef and recapture interval are present.

DISCUSSION

The density manipulation described in this paper is an attempt to use an ecological field experiment in a nonbenign, subtidal habitat to study the population processes of a spiny lobster. Practical limitations within this environment related to wave effects on drifting plant material and the need to enclose enough area to adequately provide for the foraging range of juvenile *P. cygnus* precluded the use of large enclosures which would have effectively prevented migration. Also, because of the potential mobility of *P. cygnus*, it was not possible to increase and maintain the density of juveniles above natural levels on a reef without such an enclosure. Therefore, only an experimental reduction in density was attempted:

1. Data from the visual estimates show that we were successful in reducing the number of juvenile *P. cygnus* on reef III to approximately 30% of the original, natural level by removing animals in January, February, and March 1981. Following the last removal, the estimated numbers of animals varied, but showed a slow increase over the 1-yr period of the manipulation experiment, with a mean of 36% of the original January level during March through June 1981 and a mean of 55% of the original level during October 1981 through January 1982. However, the number of juveniles on both reefs I and V, the control reefs, also declined during this period, and the population on reef V was estimated to be below that of reef III on 18 February 1981. Therefore, it is difficult to separate the effects of the systematic removals from a general decline in numbers indicated by what was observed on reefs I and V.

   The size and age structures and the sex ratios of *P. cygnus* juveniles on reefs I, III, and V in January 1981 were very similar. Size and age structures and the sex ratios of these juveniles

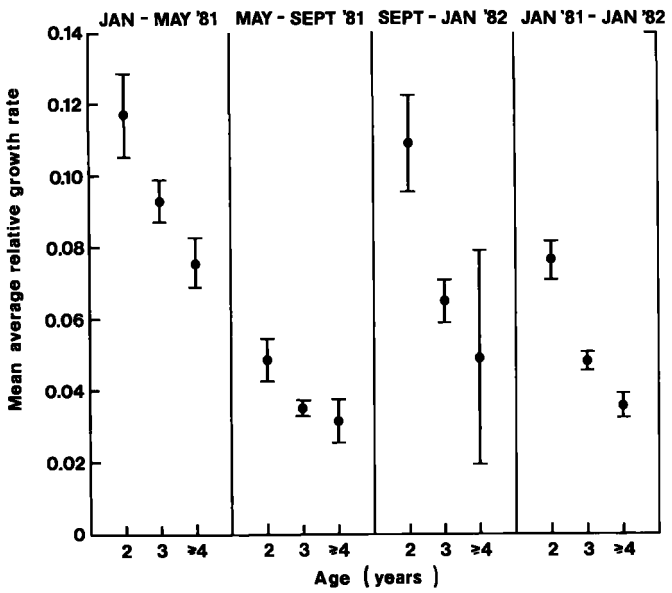

FIGURE 7.—Average relative growth rates (ARGRs) of juvenile *Panulirus cygnus* on test reefs III and V (combined) at Seven Mile Beach, Western Australia.

also were very similar among the reefs at all subsequent sampling times, suggesting that the drastic reduction in the density of *P. cygnus* on reef III, and the method of reconstituting the population, did not have an evident effect on these characteristics over the 1-yr period of the experiment.

2. The population sizes of ≥3-yr-old *P. cygnus* juveniles, estimated from catches with baited traps, were significantly lower on reef III than on reef V in January 1981 and August 1981, but were similar (i.e., not significantly different) in January 1982. However, these data, and the estimates of mortality derived from them, are subject to the usual problems associated with mark-recapture techniques. Phillips (unpubl. data) has found in more recent studies that the baited traps are capable of attracting juveniles from over a wide area and hence the population size and density estimates applied to individual reefs probably are inaccurate. However, the trends in the population estimates from the mark-recapture data are supported by the visual estimates of population size, indicating that they reflect what was actually happening on these two reefs.
3. Clearly, the visual estimates provide a more specific set of information about population levels of juveniles living on the reef. The method also allows direct estimates of numbers over short time intervals and with minimal disturbance of the western rock lobsters. However, although there is no doubt about the drastic decline in the numbers of tagged lobsters on reefs I and V after the period of initial tagging, it is not possible to determine if this was as a result of tagging mortality, an emigration as a response to handling and tagging or part of the normal behavior pattern.

Despite the attempts to select directly comparable reefs for the experiment, it is possible that reefs III and V do provide different environments for the resident *P. cygnus*. The movement of 71 individuals from reef V to reef III may be part of a typical movement from shallower to deeper reefs. It seems unlikely that water depth, per se, is the primary factor involved, because the difference in depth between the two reefs is no more than 2 m. The reefs used by Chittleborough (1970) at Garden Island, on which he found *P. cygnus* juveniles remained for several years with little movement even from one part of the reef to another, were similar in depth to reef III.

Observations during sampling indicated that on reefs I and V, which are both located close to the beach, relatively large amounts of plant detritus build up around the base of the reef and under ledges and that turbidity of the water is sometimes quite high. These effects also occur on reef III, but are less pronounced. This suggests that less favorable conditions on the shallower, inshore patch-reefs may cause some *P. cygnus* to seek reefs slightly farther offshore which have more suitable conditions. It also may help to explain the higher variability in numbers of juveniles from the visual estimates made on reef V compared with reef III. Some individuals may temporarily emigrate from areas such as reef V during periods of adverse conditions.

Survival and mortality data, which were obtained from both the mark-recapture estimates of population size and the numbers of tagged animals recaptured on the same reef, indicate that survival of *P. cygnus* juveniles was significantly higher on reef III than on reef V over the 1-yr period of the experiment. This was evident for individuals of all four age groups. It suggests that the experimental reduction in numbers of juveniles on reef III, resulting in relatively low population densities (29–61% of the original, natural number) during the 1-yr experimental period, led to significantly higher survival than on reef V, where *P. cygnus* juveniles were present at natural density levels. One explanation for this is that reduced densities of juveniles on a reef may lead to a corresponding reduction in predation mortality and adverse interspecific effects of crowding. An alternative explanation for the very high survival of *P. cygnus* juveniles estimated on reef III, relative to reefs I and V, is that the tagged juveniles on reef III remained for the entire year while many of those tagged on reef I and V emigrated to other reefs.

These mortality data are subject to several sources of error, including the basic problems associated with mark-recapture sampling to obtain population estimates (Bailey 1951). The age-specific estimates of survival obtained from comparisons of numbers of tagged individuals released on each reef in January 1981 and recaptured there in January or February 1982 requires a major assumption. It is that all of the tagged individuals not recaptured on a particular reef after one year have died. This undoubtedly is not the case because some of those individuals probably moved to other reefs at Seven Mile Beach after their release. To the extent that this occurred, the survivorship estimates are low.

No quantitative information is available to correct the estimates for this effect.

The analyses of the growth data, including both the single molt increments and the ARGRs, clearly indicated high variability in growth rates between age groups, and that site (reef) and season variations (recapture interval) were compounding factors. Estimates of growth made during the 1-yr period of the study were similar to those obtained on reef I in previous studies at Seven Mile Beach (Chittleborough 1970, 1975, 1976; Chittleborough and Phillips 1975; Joll and Phillips 1984). However, despite the fact that the population densities in 1981 were the highest ever recorded, the molt increments of the 3-yr-old *P. cygnus* were significantly higher than at the low densities in 1971–74.

Comparisons of the growth data for *P. cygnus* juveniles showed no significant differences in growth within any age group between reefs I, III, and V. The reduced densities of juveniles on reef III had no apparent effect on either their overall growth rates or their molt increments. This suggests that the food resources on the surrounding seagrass beds may not limit growth within the range of *P. cygnus* densities present on these reefs during the field experiments. However, other factors may be involved. The foraging ranges of juveniles on reef III may overlap those animals from reef V and other nearby patch-reefs. More recent acoustic tracking studies by Jernakoff (unpubl. data) suggest that this is probably the case. If so, then reducing the density of *P. cygnus* on reef III might not produce a significant increase in their growth rates, because they could still be sharing their food resources with animals from nearby reefs.

The best tests of hypotheses about the effects of limited resources are those where the densities of *P. cygnus* are experimentally manipulated in replicated experimental areas and which incorporate appropriate controls (Connell 1974; Underwood 1979). This attempt has highlighted a number of problems. Nevertheless, it may be useful to conduct modified manipulation experiments of this kind in the future. Obviously, one of the problems with the present experiment was the lack of replication, and replication should be incorporated in the design of any future experiments. This was not possible in the present study because of high time and manpower requirements associated with the use of trapping and mark-recapture techniques. Furthermore, our observations indicate that it will be extremely difficult to find a series of patch-reefs similar enough in size, structure, and other features to serve as true replicates. As has been shown in this study, even small differences in water depth, or as yet unidentified characteristics, make the selection of reefs as equivalents very difficult. Selection of such reefs also will not be easy because often several reefs are within the known foraging range of the juveniles.

Evaluation and refinement of the visual estimation technique also will be necessary before further manipulation experiments are undertaken, as the usefulness of mark-recapture techniques is dubious. Without the development of such a refined method which would permit rapid and frequent estimates of population size, the effect of subsequent changes in population levels cannot be properly monitored. Without such a method it also would not be possible to determine the extent to which migrations of *P. cygnus* juveniles to and from the reefs are induced by the use of the baited traps or by handling and other disturbances during the mark-recapture process.

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A LONG-TERM STUDY ON THE BEHAVIOR AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN THREE NATURALISTIC SUBSTRATES: EELGRASS, MUD, AND ROCKS

DIANA E. BARSHAW[1] AND DONALD R. BRYANT-RICH[2]

ABSTRACT

An 8-month study on the behavior, growth, and survival of early juvenile American lobsters, *Homarus americanus*, was conducted in three different naturalistic habitats of mud, rocks with algae, and eelgrass. Fifteen narrow aquaria (10 cm wide) allowed visual observations of American lobster's activities in five replicates of each of the three habitats. After a 3-month acclimation period to establish "natural" benthic communities which entered through the water supply, three stage IV American lobsters were introduced into each aquarium. Observations were made on the settling, burrowing, activity, and feeding behavior of these lobsters.

American lobsters in eelgrass and rock habitats settled into the substrate more quickly, had burrows a greater percent of the time, and spent less time repairing their burrows than lobsters in mud habitats. The lobsters in eelgrass had a lower mortality rate than lobsters in either rocks or mud. None of the lobsters in any substrate were observed foraging for food outside of their burrows. However, the behavior of these American lobsters indicated that they were able to capture plankton drawn into their burrows by pleopod fanning. Six lobsters molted during the coldest part of the year when the water temperature was approximately 1° to 2°C.

Stage IV of the American lobster, *Homarus americanus*, is best described as transitional between larval and juvenile (Phillips et al. 1980). During this stage major behavioral changes take place, which coincide with the morphological changes occurring in the molt. These behavioral and morphological changes cause the stage IV lobsters to descend from the upper layers of the water column to the bottom where they build a burrow (Botero and Atema 1982; Ennis 1975).

Knowledge of the American lobster's behavior from the onset of settlement until they reach a size of approximately 20 mm in carapace length (CL) remains limited because juveniles of this size range have been found in the field only sporadically.

Several laboratory experiments sought to determine the substrate preferences of stage IV American lobsters. Howard and Bennett (1979) found that lobsters (*H. gammarus*) generally choose the largest size of gravel provided (approximately 20 mm in diameter), because larger rocks have more available space between them for burrows. If given a choice between a gravel substrate or a silt/clay substrate, American lobsters prefer the gravel (Pottle and Elner 1982). In choice tests, stage IV American lobsters preferred rocks with macroalgae, followed by, in order of decreasing preference, mud, rocks on sand, and sand. If not afforded a choice, the lobsters settled most quickly on the rocks with macroalgae, followed by rocks on sand, mud, and sand (Botero and Atema 1982).

MacKay (1926) recorded observations on the lobsters' ability to burrow in mud. Subsequently Cobb (1971), Berrill and Stewart (1973), and Botero and Atema (1982) have described the methods by which juvenile American lobsters make burrows in both mud and rocky substrates. No observations have been made on American lobsters burrowing into other substrates, such as eelgrass or peat.

Cobb et al. (1983) followed stage IV *H. americanus* for short periods of time following their release into the field. They observed behavior which may indicate that American lobsters test different substrates and continue moving if they are on unsatisfactory substrates such as sand or mud; however, only two lobsters were actually seen rejecting a substrate.

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None of the previous studies lasted for more than a few days, and long-term behavioral observations have never been recorded on early juvenile American lobsters. There are virtually no field data on simple life history parameters such as their preferred substrate, growth rate, diet, and behavior. It is unwise to proceed with experimental laboratory studies on an organism without having a descriptive life history background to provide context. Both Cobb (1987) and Fogarty (1987) recognized the need for more studies on the behavior and ecology of the postsettled prerecruits used in this study. At present it is difficult to gather such information in the field. However, this study was designed in order to provide such a background by carefully creating naturalistic habitats in the laboratory. We present quantified behavioral observations, survival, and growth of early juvenile American lobsters in three different substrates: mud, rocks, and eelgrass, over an 8-mo period.

MATERIALS AND METHODS

Fifteen "ant farm" aquaria (45 cm deep × 30 cm long × 10 cm wide) were constructed to optimize our ability to observe the American lobsters inside their burrows. Five of the aquaria were two-thirds filled with cohesive mud (particle size <0.06 mm) collected from mud flats in the Woods Hole, MA area. Five of the aquaria were two-thirds filled with rocks, collected from subtidal areas in such a way that a representative distribution of rock sizes was obtained (0.1–20 mm diameter). Some of the rocks in each tank had macroalgae *Coleus* (sp.) and *Fucus* (sp.), or both growing on them. Eelgrass collected from local eelgrass beds was placed in the last five aquaria; less substrate was used in these latter tanks so that the eelgrass leaves had room to grow.

The aquaria were randomly distributed in a system which provided running, unfiltered seawater at ambient temperatures seasonally ranging from 23° to 0°C. Plankton were always visible; also the three habitats occasionally had plankton blooms, during which algae and zooplankton were plentiful. The tanks were maintained on an ambient light/dark regime with a light intense enough to keep the eelgrass alive. Removable, opaque, black plastic was placed around each aquarium to the level of the substrate to ensure that the lobster burrows were dark. To establish "natural" benthic communities, the tanks acclimated from 20 July until 16 October 1982, before beginning the experiment.

Stage IV American lobster siblings from the hatchery at St. Andrews, New Brunswick, Canada were introduced, one per day into each aquarium for 3 consecutive days. Thus, the total number of lobsters at the start of the experiment was 45, 15 per treatment. Observations were recorded continuously for the first half hour after each introduction and then for the following 1.5 hours; observations were recorded by scanning (taking an instantanious reading of the lobsters' behavior) every 10 minutes. Observations were made of the following: 1) location of the animal in the aquarium, 2) motion (walking, swimming, or resting), 3) burrowing activity (pleopod fanning, bulldozing, or digging), and 4) shape, size, and location of final burrow. This procedure was similar to that used in the substrate choice tests done by Atema et al. (1982).

During the first introduction of American lobsters into several of the tanks, mud crabs, *Neopanope sayi*, immediately consumed them. The mud crabs were subsequently removed and new American lobsters were placed into these tanks.

After the American lobsters had been introduced into each of the 15 tanks, long-term observations began of each lobster in each tank at intervals ranging from daily to twice per week. The observation periods were at different times during the day with 5.1% during the dark period, although it was difficult to see the lobsters in low light because of the cryptic nature of some burrows. There was a total of 195 observations periods. Each lobster that was visible was watched for at least one minute; if the lobster was active, observations lasted until the activity ended. However, for the quantitative analysis of lobster activity only the first minute of observations were used. A total of 495 hours of observations were made averaging 11 hours per individual lobster. For each lobster we recorded 1) the location of the lobster in relation to its burrow, 2) whether the lobster had molted, 3) the lobster's activity, and 4) the shape of the burrow (with a quick sketch). The activities observed are described in Table 1.

The experiment lasted approximately eight months, from 21 October 1983 to 1 July 1984. The lobsters were not fed during that time; we assumed they would find food from the communities in which they lived. At the end of the experiment, the surviving lobsters were weighed and their carapace length was measured. Additionally, the sediment in each tank was sieved through a 1 mm screen, and all organisms were collected, weighed, and identified to the genus or species level.

TABLE 1.—Description of the different activities observed throughout the experiment.

Activity	Description
Rest	No movement for at least 30 seconds. Grooming was not considered movement, and was not recorded separately from rest.
Pleopod fan (PPF)	Movement of the pleopods; if the fanning was being used to repair the burrows, i.e., sediment was being moved, then the activity was recorded as burrow repair.
Burrow repair (BR)	Any activity which caused sediment to be moved, including bulldozing (pushing sediment foward with the claws spread apart), pleopod fanning, and digging (loosening sediment by pushing claws into it).
Investigate (INVEST)	Standing at the entrance of the burrow with antennules out and antennae flicking.
Feed	Eating anything larger than 1 mm. Activity that looked like filter feeding was not included in this category (it was part of the pleopod fan). It is discussed in the text.
Walk	Walking on the sediment. Does not include "walking" in the burrow.
Swim	Swimming in the water column.

RESULTS

Burrowing

The American lobsters in the eelgrass and rock substrates started burrow construction more quickly than the ones in the mud substrate (1 way ANOVA, Newman-Keuls test, $P < 0.05$). There was no significant difference in the time to initial burrowing between lobsters in eelgrass and lobsters in rock substrates (Table 2A).

American lobsters used the same methods to make burrows in eelgrass as in mud and rocks. They typically started at the base of an eelgrass plant and then established a burrow under the rhizomes by pleopod fanning and bulldozing. The burrows usually had two openings although burrows were seen with from one to six openings. These openings were smaller and more difficult to see than similar openings in mud or rock substrates. Although lobsters in all substrates had burrows for the majority of the observations, because their burrow had collapsed, the lobsters in the mud substrate were without a burrow for a greater percent of the observations than the lobsters in the eelgrass or rock substrates (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.05$, Table 2B). For this analysis the lobster had to be visible; if neither the lobster nor its burrow were visible during a given observation period, that observation was excluded from the analysis.

Activity

American lobsters were not seen to forage outside of their burrows. If a lobster had a burrow, it was never seen outside of that burrow in any of the treatments during the entire experiment. During the day periods, these lobsters were seen in their burrows 1,503 times, and outside of their burrows 0 times. Therefore, by using sampling theory, one can calculate that the lobsters were spending at least 99.8% of their time during light periods in their burrows (binomial distribution, $P = 0.05$). During the night periods lobsters were seen in their burrows 103 times, outside of their burrows 0 times. Therefore, the lobsters were spending at least 97.0% of the time in their burrows during the dark (binomial distribution, $P = 0.05$). The difference between the night and day percentages is a function only of the greater number of observations made during the day.

The cumulative times that the American lobsters spent at various activities were influenced by sub-

TABLE 2.—(A) The average time in minutes that it took each lobster in the eelgrass, rock, and mud treatments to start construction of their burrow (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (B) The percent of observations throughout the experiment during which the lobsters in each substrate did not have a burrow. N varied from 160 to 68, depending on how many lobsters were visible (eelgrass vs. mud and rocks vs. mud, $P < 0.05$). (C) The average weight, in grams, and the carapace length (CL), in mm, of the lobsters in each treatment at the end of the experiment.

	A	B	C	
	Time to burrow	No burrow	Weight	and CL
Eelgrass	7.92 ± 2.02	4.70 ± 1.7	4.95 ± 0.95	18.15 ± 1.25
Rock	11.92 ± 3.22	3.82 ± 1.22	3.18 ± 0.16	15.22 ± 1.34
Mud	49.17 ± 14.08	12.2 ± 3.7	3.22 ± 1.23	15.85 ± 1.92

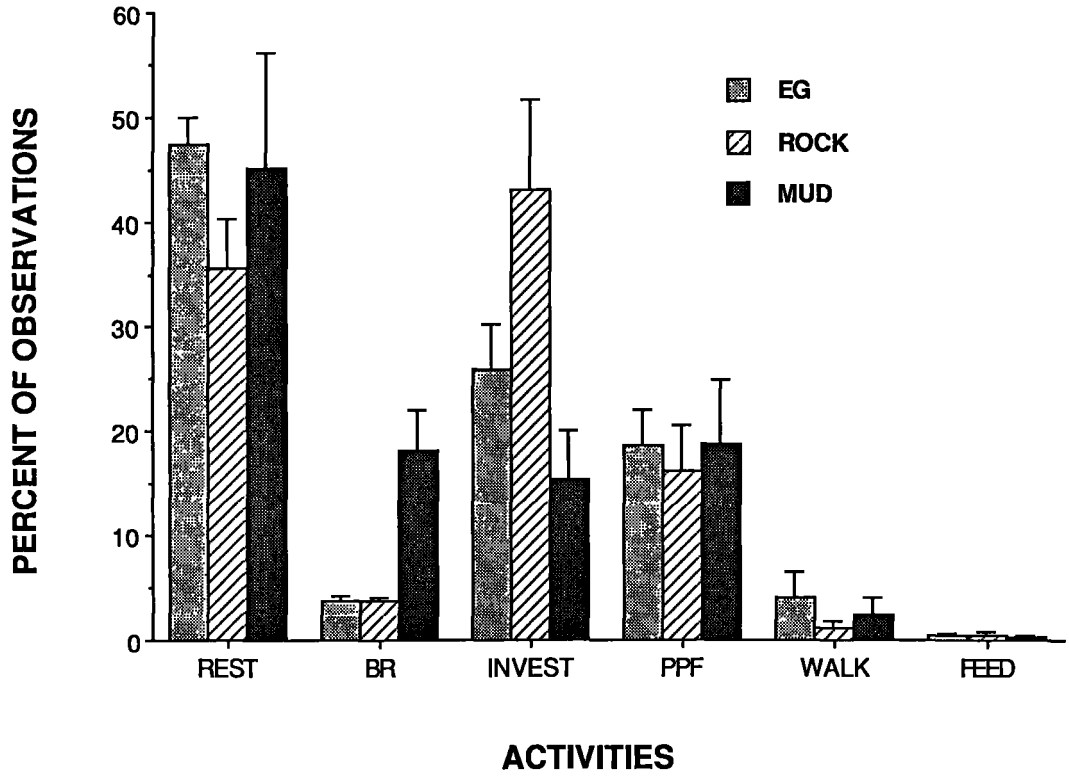

FIGURE 1.—The percent of observations in which the American lobsters were engaged in each of the listed activities. BR: eelgrass vs. mud, $P < 0.001$. Invest: eelgrass vs. mud and rock vs. mud, $P < 0.05$. N varied from 160 to 68.

strate (Fig. 1). The lobsters in the mud substrate spent a significantly greater percent of their time repairing their burrows than the lobsters in either eelgrass or rocks (arcsine transformation, 1 way ANOVA, Newman-Keuls test, $P < 0.001$). Based on percent of observations, the lobsters in mud spent significantly less time investigating than did the lobsters in rocks (tests as above, $P < 0.05$). There was no significant difference, however, between the percent of observations spent investigating in the mud vs. the eelgrass, or in the percent of observations spent investigating in the eelgrass vs. the rocks.

Based on the percent of observations, the time the lobsters spent resting and pleopod-fanning was considerable (18–45%) in all substrates and did not differ between them. Walking was only observed when a lobster did not have a burrow. Feeding occurred only on the few occasions when some edible object landed close enough to the burrow so that the lobster could reach it without entirely leaving its burrow. Twice lobsters were seen catching swimming amphipods at the entrance to their burrow.

American lobsters were observed creating a current by pleopod-fanning, which was seen to draw plankton through their burrows. During these periods the lobster stood with its clawed limbs held up and apart. The mouth parts, particularly the second and third maxillipeds moved rapidly, and the first pair of walking legs were often brought up to the mouth. Occasionally the lobster would jerk forward and snap its claws. All of the above-mentioned appendages are covered with various types of setae (Factor 1978), which could help the lobsters to catch the plankton both by "filtering" with their maxillipeds, claws, and first walking legs, and by seizing the plankton with their claws. These observations, supported by Lavalli and Barshaw (1986) and Barshaw (in press) show that American lobsters are able to catch plankton while remaining in their burrow.

Mortality

There was an initial mortality of the American lobsters in all habitats followed by no deaths in the winter and another die-off in the spring (Fig. 2). The mortality rate for American lobsters in eelgrass was significantly lower than those in the mud or in the rocks (arcsine transformation, linear, least-square regression, r^2 = 0.75 eelgrass, 0.86 rock, 0.94 mud, comparison of slopes, $P < 0.001$).

Molting and Size

At the end of the experiment there was no significant difference in the size of the lobsters between habitats, although the American lobsters in eelgrass tended to be larger (Table 2C). There was also no significant difference in the number of observed molts between treatments. We observed molting by six lobsters during the coldest part of the year when the water temperature was between 1° and 2°C.

Possible Prey

The biomass of American lobsters (>1 mm) was not significantly different among treatments, but the biomass of American lobsters in eelgrass tended to be higher (ANOVA, Newman-Keuls test, $P < 0.01$, Table 3). There were fewer different genera residing in the mud habitats, with the greatest diversity in rock.

DISCUSSION

Initial observations showed that stage IV American lobsters started to burrow more quickly in eelgrass and rock habitats. While several investigators have shown that American lobsters choose rocks over mud (Howard and Bennett 1979; Pottle and Elner 1982; Botero andAtema 1982), no choice experiments have used eelgrass as a substrate. Likewise, in this experiment we have not directly shown that the lobsters prefer the eelgrass substrate because they were not offered a choice. Speed of settling would be indicative of a preference, however, if the method that lobsters use to choose a substrate is to keep swimming if the habitat is unsuitable, but settle if it is suitable. Such behavior was observed in laboratory experiments by Botero and Atema (1982). Indications that lobsters keep swimming over unsuitable substrates was also observed by Cobb et al. (1983) in the field.

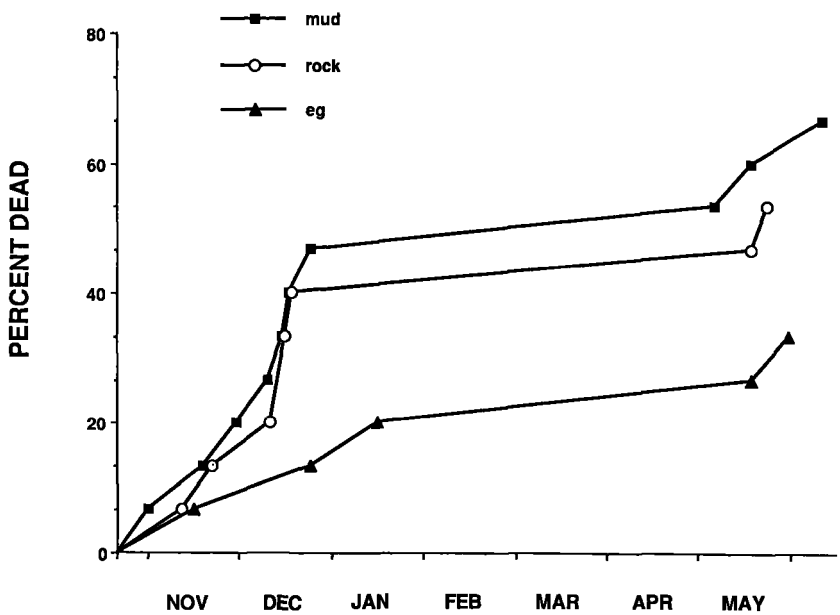

FIGURE 2.—The cumulative percent of American lobsters that died in the three treatments, each point represents a day when a lobster died. Fifteen lobsters per treatment were present at the beginning of the experiment. Eelgrass vs. mud and eelgrass vs. rock, $P < 0.001$.

TABLE 3.—Average biomass (wet weight) and species list of organisms larger than 1 mm living in the sediment of each treatment at the end of the experiment.

Treatment	Bivalve	Polycheate	Other
Eelgrass:	Mean biomass per tank = 8.2 ± 2.7 g		
	Mercenaria mercenaria *Yoldia* (spp.)	*Capitella* (spp.) *Clemenalla* (spp.) *Glycera* (spp.) *Lumbrineris* (spp.) *Neris* (spp.) *Spiondae* (gen.) *Terebellida* (gen.)	Sipunculoidea (*Golfingia gouldi*)
Rock:	Mean biomass per tank = 3.28 ± 1.07 g		
	Andora ovalis *Andora transversa* *Mercenaria mercenaria* *Mucoma* (spp.) *Yoldia* (spp.)	Chrysopetalidae (*Dysponetus pygmaeus*) *Nephytidae* (spp.) *Nereis* (spp.) *Phyllodocdae* (gen.) *Sapella* (gen.) *Terebellida* (gen.)	Sipuculoidea (*Golfingia gouldi*) Crustacea (*Neopanope sayi*)
Mud:	Mean biomass per tank = 4.4 ± 1.07 g		
	Geukendia demessus *Solemya velum* *Yoldia* (spp.)	*Glycera* (spp.) *Nephtys* (spp.) *Nereis* (spp.) *Orbiniidae* (spp.) *Terebelleda* (gen.)	

The mud substrate appeared to be the least suitable of the three tested since American lobsters in eelgrass and rocks were without burrows for less time than those in mud. However, even in the mud habitat the lobsters had burrows for an average of 87.8% of the observations (Table 2B). The three substrates used in this study were chosen partly because of their differences, yet the lobsters managed to build and maintain burrows in all three substrates for eight months. This result clearly shows that early juveniles have flexible behavior and modify it to adapt to different substrates.

The way that the American lobsters partitioned the amount of time they spent on different activities was also affected by the substrate in which they lived. While lobsters in eelgrass and rock habitats spent little time repairing their burrows, lobsters in mud spent considerable time on repair (Fig. 1). This result is consistent with the characteristics of the three substrates. Eelgrass stabilizes the underlying sediment (decreases erosion) by baffling the water currents with its leaves and binding the sediment with its roots (Scoffin 1970); rocks, although usually found in areas of stronger currents, provide a ready made solid roof; mud, however, is more easily disturbed (Rhoads and Young 1970). If one lobster did not have a burrow in the mud tanks, its walking often destroyed the other lobsters' burrows.

The extra time that the American lobsters in mud spent repairing their burrows was subtracted mainly from investigation time (Fig. 1), perhaps because there was not as much prey in the mud for the lobsters to detect, so this activity was the most expendable. No significant differences were found between the time budgets of the lobsters in eelgrass and the lobsters in rocks; however, the lobsters in eelgrass spent more time resting than investigating, while the opposite was true of the lobsters in rock substrate.

The American lobsters in the eelgrass had a lower mortality rate than those in either mud or rocks. This result could have been due to the greater biomass of possible prey animals living in the eelgrass habitat, and/or the greater complexity of the eelgrass habitat, which in essence separated the lobsters and ameliorated the effects of high density. Seagrass beds in nature have also been shown to have a greater biomass of species living in them than the biomass of species living in less complex substrates such as mud or sand (Orth 1973; Thayer et al. 1984).

The lower mortality rate of lobsters in eelgrass led to a greater number of lobsters per tank in this treatment. Higher concentrations of lobsters have been shown to cause slower rates of growth in lobster living in fairly unnatural substrates (Cobb and Tamm 1974). In this study, the American

lobsters in eelgrass were not smaller perhaps also because the eelgrass substrate ameliorated the effects of higher density. We did not observe any differences in the activity budgets of the lobsters owing to higher density (Fig. 1).

This study shows that early juvenile American lobsters differ dramatically in their behavior from older lobsters. They seldom, if ever, forage for food outside of their burrows, but instead remain inside of them. This was true even though there were no predators present other than other juveniles.

The lobsters' main activities within their burrows reflected their needs. Because they did not forage outside of their burrows, all of the early juveniles' nourishment must have been found inside of their burrow, or within reach of the entrance. Lobsters could forage on polycheates, meiofauna, and on any other organisms residing inside their burrows or draw plankton in by pleopod-fanning. In this study lobsters were seen to catch swimming amphipods at the entrance to their burrow, and Berrill (1974) observed similar behavior. Besides resting, the lobsters mainly "investigated" for anything edible in the entrance of their burrow and pleopod-fanned to draw in plankton. If they were forced to burrow in a relatively unstable substrate, such as mud, they spent a significant amount of time maintaining that burrow.

The claws of early juvenile American lobsters are smaller and weigh less relative to the abdomen than those of older lobsters, and, by external appearance the two claws are not differentiated from each other. Furthermore, the speed of the tail flip reflex is faster at sizes smaller than 20 mm carapace length (Lang et al. 1977). These morphological characteristics along with the behavioral results from this study, and field observations that juveniles become easier to find at a carapace length of 20–40 mm (Cooper and Uzmann 1980; Able et al. in press), indicate that the juvenile stage of the American lobster can actually be divided into two substages: 1) the early juvenile stage, spanning settlement to the time until claws begin to differentiate, during which period the lobsters seldom, if ever, leave their burrow; and 2) the late juvenile stage, starting when the claws are differentiated and become larger in relation to the abdomen and ending with sexual maturity. At this stage, the lobsters start to forage for food outside of their burrows, and behave more similarly to adults (Cooper and Uzmann 1980; Able et al. 1988).

We suggest the following scenario for the life history of early juvenile American lobsters. After settling onto a suitable substrate the lobsters build a burrow where they remain for the duration of the "early juvenile" substage. By catching food, both in the substrate around their burrow entrance and by drawing plankton into their burrow by pleopod-fanning, the early juvenile lobsters manage to survive without foraging outside their burrow.

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DISTRIBUTION AND ABUNDANCE OF THE BOTTLENOSE DOLPHIN, *TURSIOPS TRUNCATUS* (MONTAGU, 1821), IN VIRGINIA[1]

ROBERT A. BLAYLOCK[2]

ABSTRACT

The distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, was examined by conducting aerial surveys of the Chesapeake Bay mouth and nearshore coastal waters of Virginia in 1980 and 1981. Bottlenose dolphin density was estimated using line transect methods and a 4-term Hermite polynomial was chosen to model the detection function. Six surveys in the Chesapeake Bay mouth resulted in an average density estimate of 0.159 dolphins/km^2. Ten surveys along the southern Virginia coast produced an average density estimate of 3.446 bottlenose dolphins/km^2 within 2 km of shore. Average bottlenose dolphin abundance in the Chesapeake Bay mouth and along the southern Virginia coast was estimated at 340 dolphins (±104, 95% C.I.). An estimate of 0.208 bottlenose dolphins/km^2 along the northern Virginia coast is tenuous because only one survey was conducted there. Dolphin sightings were distributed uniformly along the southern Virginia coast with the exception of some clustering of herd sightings at the capes bordering the Chesapeake Bay mouth. The percentage of calves per herd averaged 7.5% in Chesapeake Bay mouth, 4.3% in the southern coastal area, 9.0% in the northern coastal area, and peaked in June. Five of seven bottlenose dolphins identified by unique dorsal fin shapes in 1980 were resighted in 1981, suggesting seasonal residency of individuals.

Of the 23 cetacean species occurring along the Virginia coast (Leatherwood et al. 1976; Blaylock 1985) the bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821), is the only cetacean found near shore regularly and in large numbers. However, there are few quantitative data available to assess the abundance, distribution, and seasonal occurrence of *Tursiops truncatus* (hereafter referred as *Tursiops*) in Virginia coastal waters.

Those bottlenose dolphins occurring seasonally in Virginia are believed to form part of a population distributed from northern North Carolina to New Jersey during the summer. This population was the focus of a sporadic fishery along Hatteras Island, NC from circa 1797 to 1929, the primary products of the fishery being hides and oil (True 1891; Townsend 1914; Mead 1975). From cumulative catch records, Mitchell (1975) estimated a historical population size of 13,748–17,000 dolphins and inferred annual migration from biannual peaks in catches during the fall and spring. True (1891) earlier suggested a north-south migration, reporting on fishermen's observations that bottlenose dolphins were usually seen traveling south in the fall and north in the spring, with only a few remaining near Hatteras during the summer.

Analysis of large-scale aerial surveys along the northern and mid-Atlantic U.S. coast revealed a bimodal longitudinal *Tursiops* distribution, interpreted as separate nearshore and offshore areas of abundance (CETAP 1982). These areas represent the habitats of two distinct morphological types of *T. truncatus*. The offshore type is slightly larger at the onset of physical and sexual maturity than the nearshore types and ultimately attains a greater size[3].

An important finding of the CETAP surveys was the presence of multiple latitudinal peaks in coastal sightings indicating discontinuities in the north-south distribution of nearshore *Tursiops* (CETAP 1982). These observations indicate either an uneven distribution of nearshore *Tursiops* or the presence of multiple coastal populations or subpopulations. However, a recent epidemic suggests that the U.S. east coast *Tursiops* may represent a single stock.

Tursiops mortalities south of North Carolina during autumn of 1987 increased sharply with the apparent emigration of *Tursiops* from Virginia

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waters.[4] If the high level of *Tursiops* mortalities experienced in the mid-Atlantic coast during the summer of 1987 was because of an infectious agent, then its spread to conspecifics in more southerly regions may have been caused by contact between individuals from different areas and more extensive migration than has been previously suggested.

In the present study I used aerial surveys to estimate the abundance and examine the distribution of *T. truncatus* in Virginia coastal waters, including the Chesapeake Bay mouth. I also investigated natality periods by monthly comparison of the average percentage of calves present and residency patterns using photographic records of identifiable individuals.

METHODS

Aerial surveys were conducted during July–October 1980, and May–June 1981, from a high-winged, single-engine aircraft (U6A DeHavilland Beaver[5]) at an altitude of 152 m and at an airspeed of 147 km/h. Observers sitting in the two passenger seats searched each side of the transect for bottlenose dolphins. A recorder/navigator sitting forward of the observers and next to the pilot helped to maintain predetermined transect lines and recorded sightings which were communicated via intercom.

Upon sighting a bottlenose dolphin herd, the perpendicular distance from the flight path to the herd center was determined from calibrated, taped markings on the wing struts with the aircraft in level flight or a hand-held inclinometer. The transect was then temporarily halted and the herd circled at a lower altitude to count individuals. The herd location, direction of travel, behavior, and the number of calves were also noted. Transect lengths and the survey area were measured with a digital planimeter from NOS/NOAA navigation charts.

Depending upon the area surveyed (Fig. 1), two types of survey schemes were used. Systematic, latitudinally oriented transects were used in the Chesapeake Bay mouth (CBM) during 1980. The northern starting point for each survey was randomized, and each transect was located 7.4 km south of the previous transect. Two exceptions to this regime occurred, but in neither case was the distance between transects less than 3.7 km. Three or four transects were flown during each CBM survey and each survey covered approximately 30% of the total survey area. CBM surveys were not conducted in 1981.

Longshore surveys were flown from north to south in 1980 and 1981, parallel to the coast and 1 km offshore from Cape Charles to False Cape (32.3 km). Those conducted in 1980 were flown immediately upon completing the CBM surveys so that there was no possibility of counting herds in the longshore area that were counted during CBM surveys, except perhaps during transit between Cape Charles and Cape Henry, which was flown over open water on the shortest line between the two points. One additional survey was flown along the northern Virginia coast.

After subtracting the minimum distance from the transect that could be observed because of limited visibility directly beneath the aircraft, the perpendicular sighting distance data were truncated at 1 km. Data from all three study sites were then pooled for the calculation of $g(x)$, the detection function for line transect, and $[\hat{f}(0)]$, the probability density function of perpendicular sighting distances evaluated at the transect. In line transect the detection function $g(x)$ is the conditional probability of observing an object at perpendicular distance x from the transect line and $f(x)$ is $g(x)$ scaled to integrate to one (Burnham et al. 1980). Each survey was treated as a replicate to determine the analytical variance of $\hat{f}(0)$. Herd density was then calculated separately for each of the survey areas using $\hat{f}(0)$ estimated from the pooled sightings.

Several estimates of $\hat{f}(0)$ and its analytical variance were calculated by fitting parametric and nonparametric models to the distribution of perpendicular sighting distances using the Fortran programs TRANSECT (Laake et al. 1979) and HAZARD and HERMITE (Buckland 1985). Maximum likelihood estimates and large-sample variances were found using the procedure of Burnham et al. (1980: 135–136). The Fortran program SIZETRAN (Drummer and McDonald 1987) was used to test the hypothesis of independence between herd size and perpendicular sighting distance using a likelihood ratio test and thus determine if the detection function was biased by herd size.

Herd density was estimated as (Burnham et al. 1980, p. 18, eq. 1.3):

$$\hat{D} = n\hat{f}(0)/2L$$

[4] D. M. Burn, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. June 1988.

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

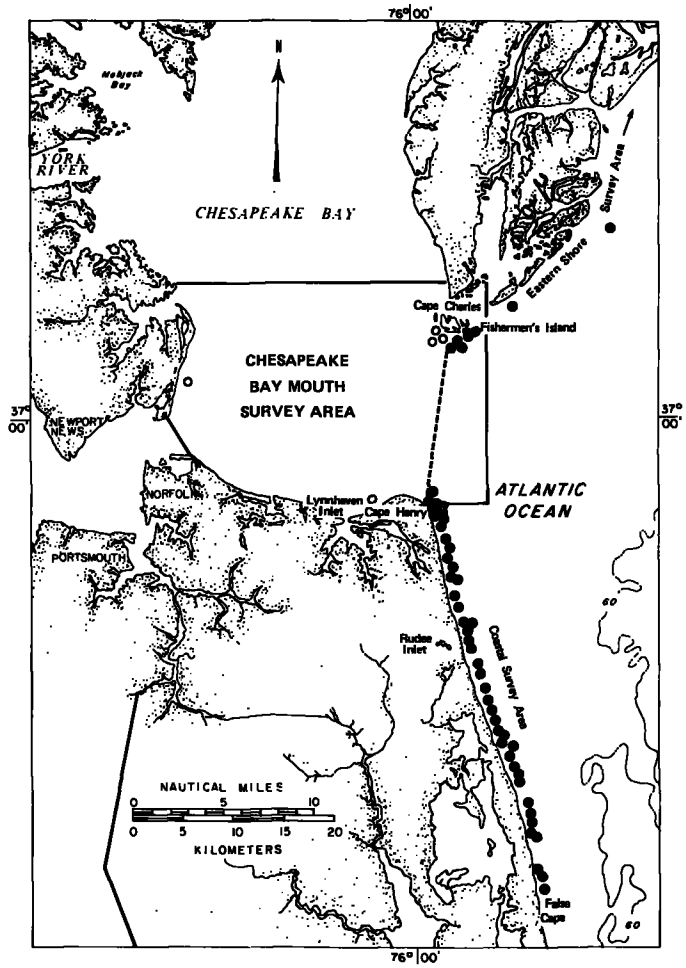

FIGURE 1.—Coastal survey areas and bottlenose dolphin sightings (closed circles) and Chesapeake Bay mouth survey area (enclosed by dark lines) with dolphin sightings (open circles). Dashed line represents transit during coastal surveys. Sightings near Fishermen's Island and Cape Henry which occurred during coastal surveys were included only in the coastal survey analyses.

where n is the number of herds detected and L is the transect length in kilometers. The variance of $\hat{D}$ was estimated as (Burnham et al. 1980, p. 51, eq. 1.17):

$$S^2(\hat{D}) = \hat{D}^2[(\hat{\text{cv}}(n))^2 + (\hat{\text{cv}}(\hat{f}(0))^2].$$

Herd size was not significantly different between study areas (Kruskal-Wallis test (K-W test), $\chi^2 = 0.9953$, df = 2, $P = 0.61$, Sokal and Rohlf 1981) and sightings were pooled to determine the overall mean herd size. Herd sizes were not normally distributed (Fig. 2) and therefore were normalized by log transformation to calculate the geometric mean (Sokal and Rohlf 1981) and its variance. Bottlenose dolphin density ($\hat{P}$) is the product of herd density ($\hat{D}$) and mean herd size ($\bar{H}$). The variance of $\hat{P}$, following Goodman (1960, p. 710, eq. 7) is

$$\hat{s}^2(\hat{P}) = \frac{\bar{H}^2 s^2(\hat{D})}{n(\hat{D})} + \frac{\hat{D}^2 s^2(\bar{H})}{n(\bar{H})} - \frac{s^2(\hat{D}) s^2(\bar{H})}{n(\hat{D}) n(\bar{H})}$$

with $n(\hat{D})$ equal to the number of herd sightings in the survey area and $n(\bar{H})$ equal to the number of herds used in the estimation of $\bar{H}$. This assumes

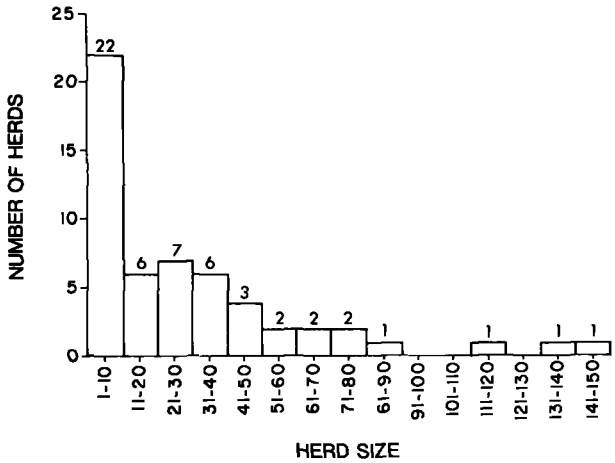

FIGURE 2.—Distribution of bottlenose dolphin herd sizes. Numbers above bars denote the number of herds in that size class.

independence between herd size and perpendicular sighting distance.

Bottlenose dolphin abundance is the product of $\hat{P}$ and the area surveyed. In the CBM area this may be extrapolated to the total area if the transects are distributed randomly with respect to dolphin sightings.

The recorder did not distinguish between observer's sightings when recording them, thus observer bias was not investigated. The effects of sea state and sun glare on detectability were not investigated. Surveys were not conducted when sea states were above two on the Beaufort scale, and it is unlikely that sea state influenced the results. However, the effect of glare reduced the observers' field of view, which decreased the number of animals detected and resulted in an underestimation of $\hat{P}$.

I conducted photographic surveys from a 7 m boat on five occasions in 1980 and six in 1981 for the purpose of identifying individual bottlenose dolphins by the shape of, or markings on, their dorsal fins. Contact prints of the 35 mm photographs were examined under a dissecting microscope at 40× magnification.

RESULTS

Six aerial surveys in the CBM averaged 119.4 km per survey, covered an area of 762 km^2, and resulted in five herd sightings of bottlenose dolphins. Ten surveys along the southern Virginia coast resulted in 49 herd sightings. Each coastal survey was 32.3 km in length and covered an area of 65 km^2. An additional survey along the northern Virginia coast was 108 km in length, covering an area of 216 km^2, and resulted in two herd sightings.

In line transect the distance at which a bottlenose dolphin herd is sighted is assumed to be independent of its size (Burnham et al. 1980; Seber 1986). Although it seems reasonable that larger herds would be detected at greater distances, analysis of herd size and sighting distance using the method of Drummer and McDonald (1987) showed no significant size-bias ($P \geq 0.05$). As a check, I also regressed herd size against perpendicular sighting distance. There was no apparent association between herd size and distance from the transect ($r^2 = 0.001$) (Fig. 3). The geometric mean herd size was 14.4 bottlenose dolphins/herd (SE = 4.0, $n = 56$).

Truncation of bottlenose dolphin sightings at 1 km resulted in the discarding of one herd sighting in the southern coastal area, none in the CBM, and one in the northern coastal area. The truncated sighting in the northern coastal area was at approximately 1,200 m from the transect and the herd was apparently feeding in the wake of a trawler, thus the sighting was atypical of other sightings during this study and probably influenced by the presence of the trawler (see Leatherwood 1975). Both sightings in this area occurred farther offshore than sightings in the other study areas.

Several parametric and nonparametric models were investigated for fit to the pooled perpendicular sighting distances (Table 1). None of the models differed significantly from the observed distance distributions (chi-square test, $P > 0.05$). The coefficient

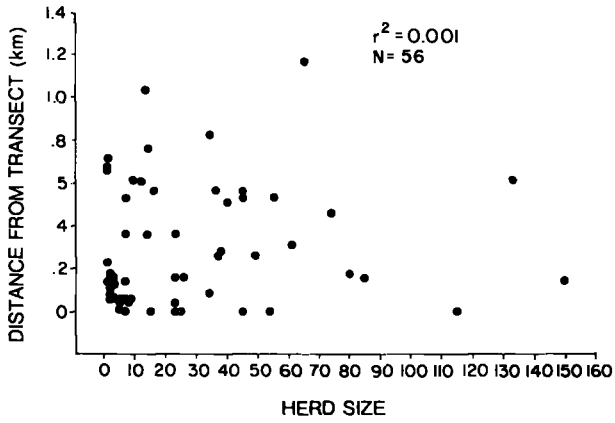

FIGURE 3.—Scatterplot of sighting distance (in kilometers) versus herd size of bottlenose dolphins. (Note that some of the points in the 1–10 size class and the interval 0–0.2 km represent more than one herd.)

TABLE 1.—Models used in calculation of the detection function $g(x)$ for bottlenose dolphin. N is the number of terms used in the model and $\hat{f}(0)$ is $f(x)$ evaluated at the transect. SE[$\hat{f}(0)$] was calculated assuming asymptotic normality with Z = 1.96.

Model	N	$\hat{f}(0)$	SE[$\hat{f}(0)$]	Reference
Hermite polynomial	3	2.849	0.441	Buckland 1985
Hermite polynomial	4	3.104	0.522	Buckland 1985
Hazard rate	na	3.004	1.345	Buckland 1985
Fourier series	4	3.323	0.551	Burnham et al. 1980
Negative exponential	na	3.216	0.936	Burnham et al. 1980
Exp. power series	2	3.649	2.198	Burnham et al. 1980
Exp. polynomial	2	3.001	0.866	Burnham et al. 1980
Half normal	na	1.950	0.398	Burnham et al. 1980

of variation of the 3-term Hermite polynomial was slightly less than that of the 4-term (0.154 vs. 0.168), but the 4-term Hermite polynomial model provided a better fit to the observed perpendicular sighting distance distribution than either the 3-term Hermite polynomial or the 4-term Fourier series models (Table 2).

The appropriate model for the observed perpendicular sighting distances should fit the data most closely near the centerline of the transect (Schweder 1977). The 4-term Hermite polynomial model closely approximates the observed sighting distances in the interval 0–200 m and also in the subsequent intervals (Fig. 4).

The nonparametric 4-term Hermite polynomial model yielded an estimate of $\hat{f}(0)$ = 3.104 (SE = 0.522). Dolphin density in the southern Virginia coastal area (3.446 dolphins/km^2) was much greater than that in the CBM area (0.159 bottlenose dolphins/km^2); however, the abundance estimates are of similar magnitude (219 vs. 121 bottlenose dolphins, respectively) due to the greater area sampled

TABLE 2.—Observed and expected distribution of bottlenose dolphin herd sightings by distance intervals perpendicular to the transect (PSD in meters) with chi-square values. Figures in parentheses are degrees of freedom. Expected values are rounded to one decimal place for clarity of presentation.

PSD (m)	Observed	4-term Hermite		3-term Hermite		4-term Fourier series	
		Expected	χ^2	Expected	χ^2	Expected	χ^2
0–200	27	27.2	0.120E-2	26.1	0.320E-1	27.4	0.698E-2
200–400	10	9.8	0.441E-2	11.1	0.117	7.4	0.913
400–600	9	9.4	0.205E-1	8.2	0.803E-1	11.6	0.593
600–700	5	4.4	0.819E-1	4.5	0.423E-1	4.9	0.273E-2
700–800	2	2.3	0.338E-1	3.3	0.819	1.9	0.197E-2
800–1,000	1	1.0	0.400E-3	0.9	0.169E-1	0.7	0.114E-2
Cumulative χ^2			0.137 (1)		1.108 (2)		1.519 (1)

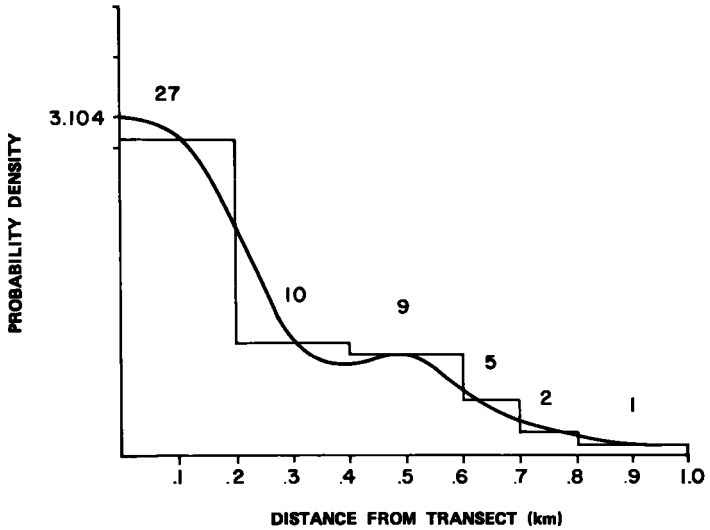

FIGURE 4.—Four-term Hermite probability density function fit to histogram of bottlenose dolphin sighting frequency and perpendicular distance (rescaled to account for the "blind spot" beneath the aircraft). Numbers above bars denote number of sightings in interval.

in the CBM (Table 3). CBM and coastal surveys were flown sequentially with no delay between them and the relatively high speed of the aircraft prevented counting of the same herd twice. Therefore, the abundance estimates in the CBM and the southern coastal survey areas may be considered additive and totaled 340 bottlenose dolphins (±104, 95% C.I.).

The survey altitude limited observations of herd composition to the percentage of calves in each herd. Bottlenose dolphins much smaller than the others and accompanied by a larger bottlenose dolphin were considered to be calves. The mean percentage of calves in all herds from all study areas peaked in June at 9.5% (SE = 0.8, n = 3) and declined thereafter until September (Fig. 5); however, there were no significant differences between months (K-W test, χ^2 = 9.1930, df = 5, $P > 0.10$). Considering the total study period, the mean percentage of calves in herds in the CBM area was 7.5% (SE = 3.2%, n = 5); in the southern coastal area, 4.3% (SE = 1.0%, n = 49); and in the northern coastal area, 9.0% (SE = 1.8%, n = 2). The mean percentage of calves in herds did not differ significantly among areas (K-W test, χ^2 = 2.8196, df = 2, P = 0.24).

TABLE 3.—Summary of aerial survey results of bottlenose dolphins. N is the number of surveys; L is the total length of transects at each location in km; and n is the number of herd sightings within one km of the transect. $\hat{D}$ is estimated herd density (herds/km^2); $\hat{P}$ is estimated dolphin density; and $\hat{A}$ is estimated dolphin abundance (standard errors in parentheses).

Survey location	N	L	n	$\hat{D}$	$\hat{P}$	$\hat{A}$	±95% C.I.
Chesapeake Bay mouth	6	717	5	0.011 (0.003)	0.159 (0.017)	121 (13)	33
Southern Virginia coast	10	323	48	0.239 (0.063)	3.446 (0.193)	219 (54)	122
Eastern Shore	1	108	1	0.014 (0.004)	0.208 (0.058)	45 (13)	—

Bottlenose dolphins were never sighted more than 1.6 km from shore during CBM surveys nor during subsequent surveys up to 8 km offshore of the coastal study area. Also, bottlenose dolphins were not found in depths greater than 10 m except in the Eastern Shore area. Plotting of bottlenose dolphin sightings (Fig. 1) shows a uniform distribution along the southern coastal area with some clusters of sightings at Cape Henry and at Cape Charles.

During 1980, seven bottlenose dolphins which were recognizable by the shape of the trailing edge of their dorsal fins were identified and photographed. In 1981, 17 individuals identified from dorsal fin photographs included 5 which had been photographed in 1980. Thus, of the 19 recognizable

individuals present during either of those two years, at least 26% were present at some time during both summers.

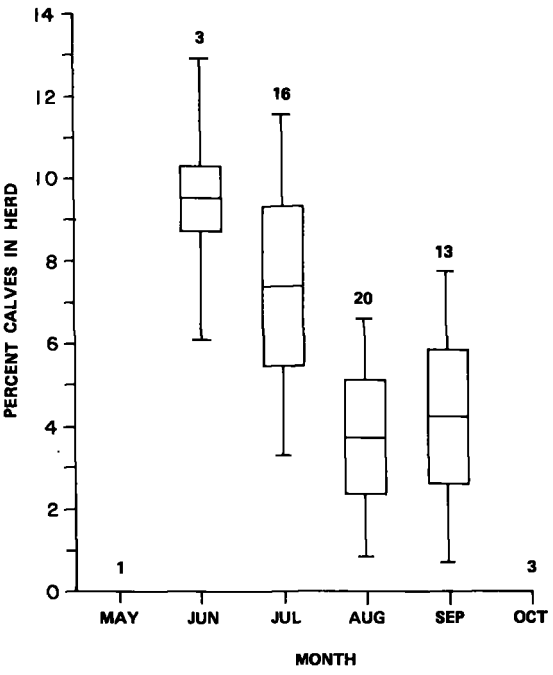

FIGURE 5.—Percentage of bottlenose dolphin calves in herds by month. Bars represent the standard error of the mean (horizontal line within bars) and vertical lines, 95% confidence intervals. Numbers above bars denote the number of herds sighted per month.

DISCUSSION

The choice of a model for $g(x)$, the probability of detecting an object at a distance x from the transect, is the primary analytical consideration in a line transect estimate of density (Burnham et al. 1980; Seber 1982, 1986). Burnham et al. (1980) thoroughly review the subject of density estimation from line transect surveys and recommended the Fourier series as a general model for $g(x)$. However, additional models which meet their criteria have since been proposed (Buckland 1985; Seber 1986). Buckland (1985) suggested the use of a model where the cosine terms in the Fourier series equation are replaced by Hermite polynomials.

Buckland (1985) warned that if the model requires four or more terms to fit the distributional data, one or more of the assumptions of line transect theory may be violated. I suggest that, in aerial surveys of cetaceans, the primary assumption that all objects on the transect are observed with a probability of one [$g(0) = 1$] is routinely violated. The diving behavior of cetaceans during different activities may vary widely, thus the probability of the animals being at the surface when the observers pass may also vary. Also, active dolphins may be more readily detected than resting dolphins. In spite of this, this assumption is somewhat less restrictive than the primary assumption of strip census which assumes that all objects within the strip are detected. If the other assumptions are met, the major consequence of failure to meet the assumption of $g(0) = 1$ is that density will be underestimated.

A further assumption is that perpendicular distances are measured without error. Even using an inclinometer, vertical motion of the aircraft and inaccuracy of the altimeter introduce error into distance measurements. Grouping distance measurements into discrete intervals is a logical way in which to compensate if the model used is robust to grouping.

The assumption of random location of transects with respect to bottlenose dolphin distribution was met by randomization of the starting point of each survey in the CBM. It is obvious from the cluster of sightings at Cape Henry and Fisherman Island that bottlenose dolphins were not distributed randomly in the coastal study area (Fig. 1). This could occur if bottlenose dolphins were counted more than once; however, their movement was slow compared with that of the observers and, because longshore surveys were flown immediately upon completion of CBM surveys, it is unlikely that dolphins were counted more than once. It is more likely that the cluster of sightings was because of an environmental factor, such as the attraction of dolphins to concentrations of prey in fronts between estuary and ocean waters.

According to Essapian (1963), mating by the bottlenose dolphin occurs in the spring and birth occurs about one year later (McBride and Kritzler 1951; Tavolga and Essapian 1957). Mead (1975), citing True (1891), stated that "Information received from the fishermen at the Hatteras fishery indicated that fetuses were generally small in September, increasing in size as the season progressed." This implies that natality occurs primarily in the spring. Townsend's (1914) data (also cited in Mead 1975) suggest an additional autumn peak in natality. The June peak in the percentage of calves agrees with those observations suggesting a spring natality peak; however, because of the slight increase in the

percentage of calves in September, a second autumn peak cannot be ruled out.

Resighting of 26% of the identifiable bottlenose dolphins in 2 successive years is evidence that some of these return to the same area. Although the probability of resighting individuals twice in 2 successive years is low if the individuals are transient, knowledge of the length of stay is required to infer seasonal residency. A study similar to that conducted on bottlenose dolphins in Argentina (Würsig and Würsig 1978) could provide information on the length of individual residency and should be considered. This would facilitate interpretation of the data presented here, as well as that gathered from currently ongoing surveys.

Because of the violation of several important assumptions, the accuracy of the density and abundance estimates reported here is difficult to assess. The CETAP (1982) summer average density estimate of nearshore *Tursiops* in the mid-Atlantic region was 0.0093 dolphins/km^2. This is much lower than my estimate of 0.159 dolphins/km^2 in the Chesapeake Bay mouth and 3.446 dolphins/km^3 in the southern coastal region. Besides differences in survey altitude and airspeed, one possible reason for this discrepancy is the larger area surveyed during the CETAP program. If the coastal *Tursiops* are generally found close to shore (within 2 km) and the area surveyed extends far beyond this distance, then the density of coastal *Tursiops* in its typical habitat will be underestimated. Alternatively, a heterogeneous coastal distribution could account for this discrepancy.

The importance of an average bottlenose dolphin density estimate which may be used as an index of abundance has recently been emphasized by an incidence of disease which resulted in the deaths of over 200 *Tursiops* along the Virginia coast and over 400 along the Mid-Atlantic Bight during the summer of 1987.[6] The rather large gap in the coastal *Tursiops* abundance data base renders assessment of the impact of the 1987 mortalities on local *Tursiops* stocks problematic. Future monitoring of the coastal *Tursiops* may provide answers as to the rate of recovery and allow assessment of the impact of future catastrophic events. A coordinated, long-term program to monitor coastal *Tursiops* abundance would permit temporal comparisons of abundance indices and provide a greater understanding of natural population fluctuations. Because the coastal *Tursiops* inhabit an area where human activity is rapidly increasing, such a monitoring program should receive high priority.

[6]J. G. Mead, Division of Mammals, Smithsonian Institution, Washington, DC, pers. commun. June 1988.

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NOTES

THE FEEDING HABITS OF TWO DEEP SLOPE SNAPPERS, *PRISTIPOMOIDES ZONATUS* AND *P. AURICILLA*, AT PATHFINDER REEF, MARIANA ARCHIPELAGO

The lutjanid snappers belonging to the genus *Pristipomoides* are among the most prized and valuable commercial fish resources in tropical and subtropical regions of the Pacific Ocean (Polovina and Ralston 1987). These fishes normally inhabit escarpments with high vertical relief. During an intensive bottom fish survey conducted at Pathfinder Reef in the Mariana Archipelago, two species of snappers, *P. zonatus* and *P. auricilla*, comprised more than 68% of the total catch (Polovina 1985). Depth of capture data on these two species demonstrated overlap in their bathymetric distribution (Polovina et al. 1985; Ralston and Williams 1988).

Numerous feeding studies have been conducted on snappers that inhabit shallow (<100 m) water; however, published information on the diets of deep slope snapper species in the tropical Pacific is nearly nonexistent (see review by Parrish 1987). Kami (1973) noted prey items for four species of *Pristipomoides* in Guam with total sample sizes ranging from one to six individuals, and Kluegel (1921) presented information on the diet of *P. filamentosus* in Hawaii based upon four fish. The present paper examines how two coexisting species, *P. zonatus* and *P. auricilla*, partition food resources. With recent efforts to expand and develop commercial fisheries for tropical snappers as well as other deep dwelling bottom fishes, there is an increasing need to recognize the resources that support these fishes. The results presented here will therefore be useful for developing fishery management strategies and will lead to a better understanding of the ecology of tropical demersal communities.

Methods

Stomach and spew samples from 106 *P. zonatus* and 72 *P. auricilla* were collected at Pathfinder Reef during an intensive fishing experiment on 10–19 April and 5–7 May 1984. Located in the Mariana Archipelago at lat. 16°30'N, long. 143°05'E, Pathfinder Reef is a circular, volcanic pinnacle rising to about 16 m beneath the surface. The fishes, ranging from 30.2 to 44.4 cm fork length ($\bar{x}$ = 38.4 cm, standard deviation = 2.81), were caught with hook and line on hydraulic-powered gurdies. The terminal rig and gurdy specifications are described in Uchida and Uchiyama (1986). While fishing, the vessel was usually allowed to drift over the banks and steep slopes, targeting species in the 150–275 m depth range. Our study species were captured mainly in depths between 180 and 220 m. Fishing was conducted around the entire perimeter of the bank during daylight hours (Polovina 1986).

Typical of feeding studies conducted on deepwater species with swimbladders, regurgitation of stomach contents posed serious problems (Bowman 1986). The rapid ascent to the surface forced most of the stomachs to evert and lose an unknown quantity of the contents. Many food items, however, were caught in the throat or gill rakers, picked out, and saved. These items, referred to as spews, and full stomachs were frozen and returned to the laboratory for analysis.

Laboratory procedures for examination of the samples were similar to those employed by Harrison et al. (1983). Briefly, food samples were sorted, counted, and identified to the lowest practical taxon. The volume of prey items was measured by water displacement. Fishes were predominantly identified by osteological and external anatomical characters and morphometrics. Invertebrates were identified by undigested hard parts and external morphological features including shells for gastropods and exoskeletons for crustaceans.

To analyze the data, we used percent frequency of occurrence to provide a qualitative picture of the food spectrum and percent volume of prey to describe relative biomass of prey items (Hyslop 1980). Because a high percentage of the diets was composed of urochordates, we did not employ any numerical analysis of the prey items. These pelagic, colonial tunicates (all *Pyrosoma* spp.) did not occur in discrete units and were thus difficult to count.

An interspecific comparison of the two snapper species requires some measure of diet overlap and niche breadth. Diet overlap (C_λ) was computed by using the formula developed by Morisita (1959) and

modified by Horn (1966). C_λ is formulated as

$$C_\lambda = \frac{2 \sum_{h=1}^{s} p_{ih} \cdot p_{jh}}{\sum_{h=1}^{s} p_{ih}^2 + \sum_{h=1}^{s} p_{jh}^2};$$

where p_{ih} and p_{jh} are the biomass proportions of a prey item h in the diets of species i and j, respectively, and s is the total number of major prey taxa in the food spectrum. C_λ varies from zero, when there is no overlap between the diets of species i and j, to one, when all prey items are in equal proportions. Niche breadth (B) for each species was computed by using the formula developed by Levins (1968):

$$B_i = \frac{1}{\sum_{h=1}^{s} p_{ih}^2};$$

where again, p_{ih} is the biomass proportion of a prey item h in the diet of species i and s is the total number of major prey taxa. The breadth values range from one, when prey items consist only of one category, to s, when all food items are in equal proportion in the same diet. These breadth values were then normalized as $B_n = B/s$, which ranges from a value of zero, representing the most uneven distribution of prey composition in the diet, to one, representing a totally even distribution. For the calculation of both breadth and overlap indexes, only prey items identified at least to the family level were used.

Results

The diets of *P. zonatus* and *P. auricilla* differed considerably from each other (Table 1). By volume, the 106 food samples from *P. zonatus* collected for this study were composed of 59.0% invertebrates and 41.0% fishes. The dominant invertebrate prey included the pelagic tunicate *Pyrosoma* spp. and galatheid crabs, nearly all *Munida japonica*. The most frequently occurring fishes in the diet were the ophichthid eel, *Shultzidia johnstonensis*, and the symphysanodontids *Symphysanodon maunaloe* and *S. typus*. In general, *P. zonatus* preyed heavily upon benthic organisms. Many of the prey items, such as echinoderms, octopods, and the various benthic crustaceans, must have been captured at the substratum. Conversely, the 72 food samples from *P. auricilla* were composed of 88.2% invertebrates and 11.8% fishes by volume; all were predominantly pelagic forms. Major invertebrate prey included the pelagic heteropod *Atlanta* spp., the pelagic tunicate *Pyrosoma* spp., and numerous species of cavolinid pteropods. Few fishes, most of them small and unidentifiable, were eaten by this snapper species.

The dietary overlap value (C_λ) was calculated to be 0.04. Based on the Langton (1982) convention of 0.00–0.29 as the low overlap, 0.30–0.60 as the medium overlap, and >0.60 as the high overlap, very little overlap occurred between the diets of the two snappers at Pathfinder Reef.

The niche breadth values (B) calculated for the two species indicated *P. zonatus* had a higher food breadth (3.82, s = 10) than *P. auricilla* (2.05, s = 6), suggesting more food specialization among the latter. Evenness in the proportion of the diet attributed to each prey type, however, was similar for the two species (B_n = 0.38 in *P. zonatus*; B_n = 0.34 in *P. auricilla*).

Discussion

As previously mentioned, a few fragmentary reports (cf. Parrish 1987) from various localities have addressed the trophic relationships of any tropical snapper inhabiting waters deeper than 100 m. He further attributes this lack of information to the normally remote fishing localities and, most of all, to the loss of stomach contents through regurgitation during capture.

The problem of regurgitation has plagued trophic studies of demersal fishes, regardless of whether fishing involved trawls (Mauchline and Gordon 1984; Clark 1985; Bowman 1986) or hook and line (Kluegel 1921; Forster et al. 1970; Seki 1984). Likewise, most food samples for our study were salvaged, regurgitated spewings retained in the mouth, throat, or gill rakers of the fishes. It is possible that the material occurring as spews may consist predominantly of certain prey items more likely retained because of size or some morphological structure, thereby resulting in a biased interpretation of the diet. We nevertheless employ the assumption that what is recovered is representative of the diets at the time of capture.

Based upon depth of capture information, *P. zonatus* and *P. auricilla* occupy nearly the same habitat, and considerable spatial overlap occurs in their foraging zones (Polovina 1986; Ralston and

Williams 1988). During submersible dives at Johnston Atoll, Ralston et al. (1986) verified this cohabitation with visual observations of the two species. *Pristipomoides zonatus* were observed between 215 and 250 m (median, 230 m) and *P. auricilla* between 205 and 295 m (median, 240 m). Our dietary analysis suggests that these two demersal species partition food resources by selecting prey from different microhabitats. *Pristipomoides zonatus* is best described as a demersal carnivore, with its diet containing benthic and demersal invertebrates together with tunicates and small fishes. In contrast, *P. auricilla* feeds primarily on large pelagic plankton, as evidenced by the abundance of heteropods, pteropods, and tunicates among the prey items. Kami (1973) also found tunicates (*Pyrosoma* spp.) in four of the five *P. auricilla* food samples in Guam. The differences in diet composition are consistent with the suggestion, based upon catch rates and the taking of a baited hook, that *P. zonatus* is the more aggressive predator of the two species (Polovina 1986).

Although our study revealed little overlap between the diets of *P. zonatus* and *P. auricilla*, the common occurrence of *Pyrosoma* spp. in the diets of both species seems significant. Similarly, these tunicates were also found among the stomach contents of three other congeneric species (Kami 1973; Parrish 1987). Kashkina (1987) reported intensive predation on pyrosomes, as well as salps, among

TABLE 1.—Diet composition of *Pristipomoides zonatus* and *P. auricilla* at Pathfinder Reef, Mariana Archipelago.

	Pristipomoides zonatus (*N* = 106)		*Pristipomoides auricilla* (*N* = 72)	
Species	% volume	% frequency	% volume	% frequency
Invertebrates				
Hydrozoa				
Siphonophora	—	—	3.2	20.8
Ctenophora	0.3	0.9	—	—
Polychaeta	0.3	0.9	5.4	15.3
Gastropoda	0.1	0.9	0.3	4.2
Atlantidae	—	—	0.9	12.5
Cavolinidae	0.2	4.7	38.1	72.2
Cephalopoda	0.3	0.9	7.4	2.8
Teuthoidea	—	—	0.2	1.4
Octopoda	0.1	0.9	—	—
Crustacea	2.6	10.4	5.5	44.4
Stomatopoda	0.3	0.9	0.3	1.4
Euphausiacea				
Euphausiidae	—	—	0.7	4.2
Decapoda				
Caridea	0.5	2.8	0.3	2.8
Pandalidae	1.2	2.8	—	—
Palinura	—	—	0.7	1.4
Anomura				
Galatheidae	19.6	28.3	—	—
Brachyura	17.1	13.2	0.2	1.4
Echinodermata				
Ophiuroidea	0.1	0.9	—	—
Tunicata				
Pyrosomatidae	16.3	34.9	25.0	37.5
Fishes				
Osteichthyes				
(Unid. fishes)	16.3	22.6	8.7	16.7
Anguilliformes	8.2	7.6	—	—
Ophichthidae	8.6	10.4	—	—
Myctophiformes	—	—	2.5	1.4
Ophidiiformes				
Ophidiidae	0.1	0.9	—	—
Perciformes				
Serranidae	4.0	1.9	—	—
Symphysanodontidae	3.1	5.7	—	—
Chaetodontidae	0.1	0.9	—	—
Gempylidae	—	—	0.6	2.8
Tetraodontiformes				
Balistidae	0.6	0.9	—	—

numerous pelagic and demersal fish species. Originally thought to be of little nutritional value, these tunicates have been found to contain filtered concentrations of phytoplankton and microzooplankton, thereby elevating the preys' food value. Regional and highly localized oceanographic processes will affect the distribution of such potential planktonic prey, and exploitation of these resources may influence the local distribution of predator species (Brock and Chamberlain 1968; Bray 1981). Deepwater snappers are most abundant on slopes of upcurrent exposure and near underwater headlands at Johnston Atoll (Ralston et al. 1986). These abundance patterns were attributed to planktonic concentrations created by mesoscale oceanographic processes as noted with other fishes on bank or slope habitats (Isaacs and Schwartzlose 1965; Pereyra et al. 1969).

Polovina (1986) suggested that fishing may selectively deplete one species, such as *P. zonatus*, preferentially over another (*P. auricilla*) and thereby alter the species composition in a given locality. With the small degree of dietary overlap between the two species in this study, such selective removal of *P. zonatus* will decrease predation pressure on the demersal prey resources of this species and, as evidenced in Larson (1980), may ultimately allow greater niche breadth for coexisting predator species.

In conclusion, this study has provided qualitative insight into dietary habits of two sympatric, deepwater species and has permitted some inferences regarding their ecology. Much more study is needed to comprehend fully the role of these predators in the ecosystem. Logistical constraints, including the problem of regurgitation, will continue to make quantitative assessments of diet a difficult task until new capture methodologies are developed. However, the rewards in improved understanding of deepwater ecology and increased ability to manage these valuable stocks suggest that the efforts will be justified.

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SEASONALITY AND DEPTH DISTRIBUTION OF LARVAL FISHES IN THE NORTHERN GULF OF MEXICO ABOVE LATITUDE 26°00′N

Justification and Methods

Information on early life stages of fishes is important for a better understanding of recruitment processes and for the proper management of fisheries. Knowledge of seasonal occurrence and depth distribution of larval fishes is essential for planning and scheduling ichthyoplankton cruises (Colton et al. 1979) and juvenile surveys, so that sampling for target species can be concentrated during periods and at depths where effort will be most effective (Saville 1964). In addition, knowledge of the seasonal occurrence of early life stages is an important aid in identifying larvae. Because eggs and yolk-sac larvae are planktonic for only a relatively few days after being spawned, the presence and distribution of early life stages also suggests proximity of adult spawning concentrations (Houde 1974), aiding the definition of spawning areas and seasonal spawning migrations of adults. Since some commercial and recreational fisheries (e.g., red drum, *Sciaenops ocellatus*, and black drum, *Pogonias cromis*) exploit spawning aggregations, encroachment on these aggregations could have an adverse impact on the fishery.

Colton et al. (1979) summarized larval seasonality data and spawning areas for marine continental shelf fishes between Nova Scotia and North Carolina; whereas, Herrema et al. (1985) inferred spawning seasons of coastal fishes off eastern Florida based on examination of enlarged gonads. The seasonal occurrence of larvae of many species from the northern Gulf of Mexico (GOMEX), however, is not well documented. The northern GOMEX is herein defined as waters north of lat. 26°00′N; this area approximates the U.S. Fishery Conservation (i.e., Exclusive Economic) Zone. For discussion, the study area was subdivided into three regions (Fig. 1) based on longitude as follows: eastern GOMEX (waters east of long. 86°00′W), central GOMEX (those between 86°00′W and 94°00′W), and western GOMEX (waters west of 94°00′W). Seasonality data are scattered throughout the grey literature, and many studies have focused on either select taxa or are limited in spatial or temporal coverage. The most comprehensive studies of the larval ichthyofauna community in the northern GOMEX were those of Houde et al. (1979) from continental shelf waters

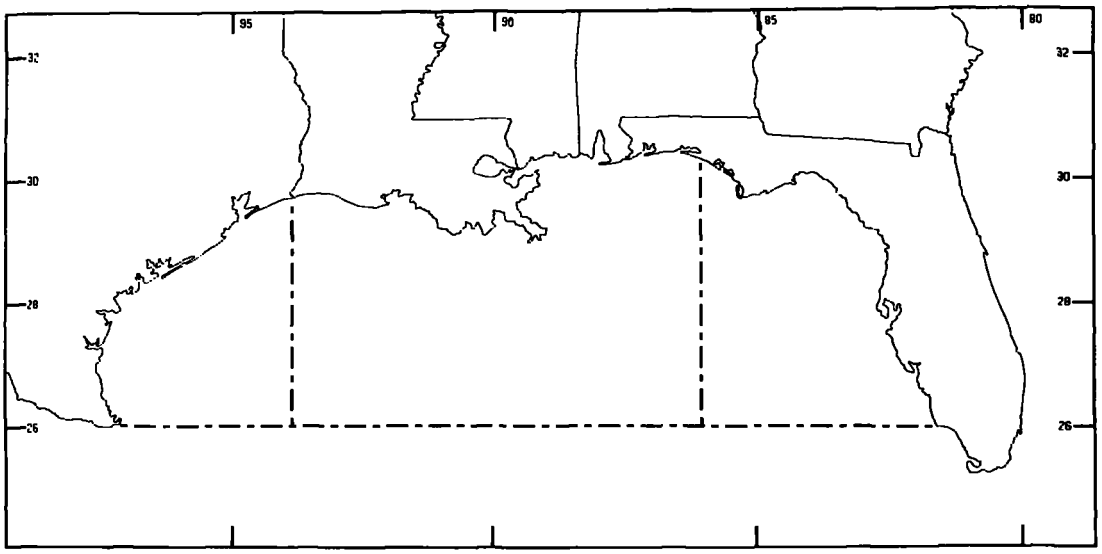

FIGURE 1.—Location of the northern Gulf of Mexico (GOMEX) and its subregions. Studies conducted in waters east of long. 86°00'W are considered northeastern GOMEX, those between 86°00'W and 94°00'W are north-central GOMEX, and west of 94°00'W are northwestern GOMEX.

off west Florida, and Finucane et al. (1977, 1979b) from the south Texas outer continental shelf. Ditty (1986) presented data on seasonality of larval fishes from neritic continental shelf waters off Louisiana that included a discussion of peak seasonal occurrence of abundant taxa; however, those data were limited in areal coverage, and there were significant gaps in the temporal occurrence of many taxa. Therefore, data on larvae of approximately 200 coastal and oceanic fishes from 61 families were compiled from unpublished plankton surveys[1], as well as other published studies from throughout the northern GOMEX, to further clarify the seasonality and peak seasonal occurrence (Table 1), and depth distribution (Table 2) of larval fishes from this area. Since the occurrence of early developmental stages of fishes suggests recent spawning (Colton et al. 1979; Ruple 1984), only studies that primarily collected larvae <10 mm SL were used. Because the taxonomy of larvae of many northern GOMEX fishes (e.g., most exocoetids, blennies, and gobies) are poorly understood, no attempt was made to compile seasonality or depth distribution data for these taxa or for anguilliform, myctophiform, or salmoniform fishes; other poorly understood taxa (e.g., engraulids and cynoglossids) were assigned only to genus.

[1]Louisiana Department of Wildlife and Fisheries, P.O. Box 98000, Baton Rouge, LA 70898-9000.

Discussion

Although not all northern GOMEX ichthyoplankton studies were readily comparable because of differences in gear and tow type, plankton net mesh size, and seasonal and areal coverage (Table 3), few major discrepancies in either seasonality or peak seasonal occurrence of larvae resulted from such differences. For example, Pearson (1929) suggested a secondary spawning from late July to November for black drum off Texas, but these dates have not been reported from elsewhere in the literature. Likewise, Finucane (1976) reported round scad, *Decapterus punctatus*, <6 mm SL in December–January, but based on sampling at the same location in subsequent years (Finucane et al. 1977, 1979b) and the seasonal occurrence of this species as suggested by others (Table 1), these may have been larvae of the rough scad, *Trachurus lathami*, rather than those of round scad. Houde et al. (1979) collected larvae of Spanish sardine, *Sardinella aurita*, during all months of their Florida continental shelf survey; however, their winter occurrences of Spanish sardine were only from the southern part of the survey area (i.e., <26°00'N). This may account for the dis-

TABLE 1.—Seasonality (X) and peak seasonal occurrence (*) of larval fishes (<10 mm SL) in the northern Gulf of Mexico (GOMEX) above lat. 26°00′N. Sources 1–31 and 75 are studies conducted in the northeastern GOMEX (waters east of long. 86°00′W); 33–59 and 74, north-central GOMEX (those between 86°00′W and 94°00′W); 61–73, northwestern GOMEX (waters west of 94°00′W); and 23, 25, 32, 48, 60, and 76–80 are Gulf-wide studies. Assignment of taxa to Families follows Robins et al. (1980) except *Epigonus* sp. and *Symphysanodon typus* which follows Johnson (1984). Numbers in Source, see end of table.

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
Elopidae	*Elops saurus*	X	X	X	X	X		X		X	X	X		1,2,41,54,61,63,66
Albulidae	*Megalops atlanticus*						X	X	X					2,6
	Albula vulpes					X	X							54,66
Clupeidae	*Brevoortia* spp.	X	X	X	X	X					X	X	X	1–3,61–63
	B. patronus	*	*	X	X					X	X	X	*	33,40–42,46,47,49,53,55, 57–59,61–63,66,69,74
	B. smithi	X	X	X									X	5,55
	Etrumeus teres	*	*	*	X	X	X					X	X	2,5,12,29,40,41,43,50–52, 59,61,63,66,68
	Harengula jaguana			X	X	*	*	*	*	X	X	X		1–3,5,30,40,46,47,50–53, 56–59,61–63,66,68,69
	Opisthonema oglinum			X	X	*	*	*	*	X	X	X		2,5,31,40,46,50–52, 56–59,61–63,68,69
	Sardinella aurita			X	X	X	X	X	X	X	X	X		2,22,50–52,56,59,61, 63,68
Engraulidae	*Anchoa* spp.	X	X	*	*	*	*	*	*	*	X	X	X	1–3,23,25,40,41,46,47, 53,56–59,61–64,66,68,69
	Anchoviella / Engraulis	X	X	X	X	X	X	X	X	X	X	X	X	40,41,46,61–63,68
Gobiesocidae	*Gobiesox strumosus*	X	X	*	*	*	X	X	X	X	X	X	X	1,3,40,41,46,47,56,58, 59,66,68
Ogcocephalidae	*Ogcocephalus* sp.					X			X	X				68
Bregmacerotidae	*Bregmaceros atlanticus*	X	X	X	X	X	X	X	X	X	X	X	X	2,4,40,59,61–64,68
	B. cantori	X	X	X	X	X	X	X	*	*	*	*	X	2,4,40,59,64
	B. houdei	X	X			X	X	X	*	*	*	*		2,4,64
	B. macclellandi	X	X			X			X	X	X	X		2,4
Gadidae	*Urophycis* spp.	X	X	X								X	X	2,40,41,57,59,61–63,68
	U. cirrata	X												64
	U. floridanus	X	X											63
Ophidiidae	*Brotula barbata*	X										X	X	40,59,64
	Lepophidium spp.	X	X	X	X	X	X	X	X	X	X	X	X	18,40,59,63,68
	Ophidion spp.	X	X	X	X	X				X	X	X	X	40,59,61–63,68
	O. selenops		X	X	X	X	X	X	X	X	X	X		18,40
	Ophidion Type 1		X	X	X	X	X	X	X	X	X	X		18
	Ophidion Type 2		X	X	X	X	X	X	X	X	X	X		18
	Otophidium omostigmum		X	X	X	X	X	X	X	X	X	X		18,68
Carapidae	*Carapus bermudensis*	X	X			X	X	X	X	X	X	X		2,63
	Echiodon sp.	X	X		X	X	X	X	X	X	X	X		2,64
Exocoetidae	*Hemiramphus balao*		X						X			X		2
	H. brasiliensis					X	X	X						2
	Hyporhamphus unifasciatus	X	X			X	X	X	X	X		X		2,40,69
Belonidae	*Ablennes hians*							X			X			62
Atherinidae	*Membras martinica*				X	X	X	X						2,40,41,46,47,58,69
Holocentridae	*Adioryx vexillarius*											X		2
	Holocentrus sp.					X								40
Caproidae	*Antigonia* spp.		X			X			X			X		2
	A. capros								X					2
Trachipteridae	*Trachipterus* sp.		X											59
Fistulariidae	*Fistularia* sp.					X								2
Centriscidae	*Macrorhamphosus scolopax*	X	X											2,40,41,59,63,64
Serranidae	*Anthias* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,41,61,63,64
	Centropristis spp.	X	X	X	X	X		X		X	X	X	X	41,53,59,61–64,68
	C. striata	X	X	X		X				X	X	X		2,7
	Diplectrum spp.	X	X	X	X	*	*	*	*	X	X	X	X	53,59,61–64,68
	D. formosum	X	X	X	*	*	X	X	*	*	X	X		2,7
	Epinephelus spp.	X	X			X	X	X	X	X	X	X		2,64,68
	Gonioplectrus hispanus									X				64
	Hemanthias aureorubens	X	X			X	X	X	X			X		2
	H. leptus		X											2,40
	H. vivanus	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,64
	Holanthias martinicensis										X	X		64
	Liopropoma spp.	X			X	X	X	X	X	X	X	X		2,61,63,64
	Myctoperca spp.				X									64
	Plectranthias garrupellus											X		2
	Serraniculus pumilio					X	*	*	*	*	X	X		2,7,40,61–63
	Serranus spp.	X	X		X	X	X	X	X	X	X	X	X	2,63,64,68

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
Grammistidae	*Pseudogramma gregoryi*					X	X	X						2
	Rypticus spp.		X			X	X	X	*	*	X	X		2,7,40,53,61–63,68
	R. saponaceus					X	X	X	X	X				61–63,68
Priacanthidae	*Priacanthus* spp.	X	X	X	X	X	X	X	X			X		2,32,64
	P. arenatus					X								64
	P. cruentatus					X				X				64
	Pristigenys alta						X	X	X	X				2,32
Apogonidae	*Apogon* sp.							X						41
Epigonidae	*Epigonus* sp.											X		64
Malacanthidae	*Caulolatilus* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,64
	C. cyanops	X								X				2
Pomatomidae	*Pomatomus saltatrix*				X						X	X	X	40,59,61,63,64,67
Rachycentridae	*Rachycentron canadum*				X	X	X	X	X	X				2,37,62,63
Carangidae	*Alectis crinitus*							X	X	X	X			48,62
	Caranx sp.	X	X	X	X	X	X	X	X	X	X	X	X	2,8,61,63,68,69
	C. crysos			X	X	X	*	*	*	X	X	X		2,8,24,41,50–52,61
	C. hippos/latus				X	X	X	X	X					32,48,60,69
	Chloroscombrus chrysurus				X	X	*	*	*	*	X			1–3,8,40,41,46,47,50–53, 56–59
	Decapterus punctatus			X	*	*	*	*	*	*	X	X		2,8,10,24,40,50–53,59, 61–63,68
	Elagatis bipinnulata					X	X	X	X	X	X			2,56,59
	Hemicaranx amblyrhynchus					X	X	X	X	X	X			48,66
	Oligoplites saurus				X	X	*	*	*	X	X	X		1–3,8,10,32,40,41,46,48, 53,56,59–61,68,69
	Selar crumenopthalmus				X	X	X	X	X	X	X			32,40,48,53,59,60
	Selene spp.					X	X	*	*	*	X	X		2,8,10,32,40,41,48,53, 59–61,63,68
	Seriola spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,8,32,40,48,56,59,60, 63,68
	Trachinotus spp.				X	X	X	X	X	X				2,8,32,47,48,61,63
	T. carolinus					X	X	X	X					32,41,48,60,66
	T. falcatus/goodei				X	X			X					48,60
	Trachurus lathami	*	*	X	X	X						X	X	2,8,23,40,41,50–52,59, 61–63,68
Coryphaenidae	*Coryphaena* spp.					X	X	X	X	X	X	X		2,41,61,64
	C. equisetis				X	X	X	X	X	X	X			2,17,23,25,40
	C. hippurus		X	X	X	X	X	X	X	X	X	X		2,17,23,25
Lutjanidae	*Etelis oculatus*							X	X	X	X	X		62,63
	Lutjanus spp.				X	X	*	*	*	X	X	X		2,40,53,59,61,63,64
	L. campechanus					X	X	X	X	X	X	X		62,64,73
	Pristipomoides aquilonaris		X			X	X	X	X	X	X	X		2,64
	Rhomboplites aurorubens	X				X	X	X	X	X	X	X		2,64
Acropomatidae	*Symphysanodon typus*		X			X						X		2
Gerreidae	*Eucinostomus* spp.				X	X	X	X	X	X	X	X		40,47,53,59,61–63,66
Haemulidae	*Haemulon* spp.					X	X	X	X					61,63
	Orthopristis chrysoptera	X	X	*	X	X								2,40,46,47,59,66,69
Sparidae	*Archosargus probatocephalus*	X	*	*	*	X								1,2,40,47,48,53,59,60, 69,70
	Diplodus holbrooki	X	X	X	X	X								2,68
	Lagodon rhomboides	*	*	X	X						X	X	*	1–3,11,40,41,46–48,53, 56,57,59,60,62,63,66,68, 69
	Pagrus pagrus	X	X			X								2,68
	Stenotomus caprinus	X											X	48,61
Sciaenidae	*Bairdiella chrysoura*			X	*	*	*	*	*	X	X			1–3,32,39–41,46,47,53, 57–59,62,63,66,69,71
	Cynoscion arenarius		X	*	*	X	X	*	*	X	X			1–3,32,34,35,39,40,46, 53,56–59,61,63,68,69,71
	C. nebulosus		X	X	*	*	*	*	*	X	X			1–3,32,35,39–41,46,47, 53,56–59,68–72
	C. nothus					X	X	X	X	*	*	X		2,32,39–41,46,53,56,59, 61–63,68
	Larimus fasciatus				X	X	X	X	X	*	X	X		34,39–41,46,53,56,58,59, 61–63,69
	Leiostomus xanthurus	*	X	X	X						X	X	*	1–3,34,39–41,44,46,47, 53,56–59,61–63,66, 68–71,74

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
	Menticirrhus spp.		X	X	X	X	X	X	X	X	X	X	X	1–3,32,34,39–41,46,47, 53,56–59,61–63,66,68,69
	Micropogonias undulatus	*	X	X	X					X	*	*.	*	1–3,34,39–41,44,46,47, 53,56–59,61–63,66, 68–71,74
	Pogonias cromis	X	*	*	*	X							X	1–3,34,39,40,46,47,56, 58,59,61,63,66,68–70,72
	Sciaenops ocellatus								X	*	*	X		1,28,39,40,46,47,53,56, 58,59,61,63,66,69,70,72
	Stellifer lanceolatus				X	X	X	X	X	X	X			32,39–41,46,53,56–59, 66,69
Mullidae	*Mullus auratus*					X								2
Kyphosidae	*Kyphosus* spp.	X	X		X	X	X	X				X		2,61,63
Ephippidae	*Chaetodipterus faber*				X	X	*	*	*	X				40,41,46,47,53,56,57,59, 61–64,66,68
Pomacentridae	*Abudefduf saxatilis*							X						63
Mugilidae	*Mugil* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,61,63,68
	M. cephalus	*	*	X	X						X	X	*	40,41,44,47,53,57,59, 61–64,69,71
	M. curema				X	*	*	*	X					40,46,47,57,59,63,64,68
Sphyraenidae	*Sphyraena* spp.				X	X	*	*	*	X	X	X		40,46,53,57,59,61–64,66, 68
	S. barracuda					X	X	X	X	X				2,64
	S. borealis		X	X	X	X								2,61,68
	S. guachancho					X	X	X	X	X				2,61,63
Polynemidae	*Polydactylus octonemus*				X									64
Opistognathidae	*Lonchopisthus macrognathus*					X								68
	Gnathagnus egregius	X	X											63
Callionymidae	*Callionymus* spp.					X				X				61,68
	C. bairdi	X												59
	C. pauciradiatus									X	X	X		40,59
Microdesmidae	*Microdesmus* spp.			X	X	X	X	X	X	X	X	X		2,40,46,57,59,61–64,68
Acanthuridae	*Acanthurus* spp.	X	X			X			X	X	X	X		2,64
Gempylidae	*Gempylus serpens*				X							X		2,61
	Nealotus tripes	X						X						2,41
	Nesiarchus nasutus	X	X									X		2,59
	Diplospinous multistriatus	X	X	X	X	X	X	X		X		X	X	2,40,41,59,61,63
Trichiuridae	*Lepidopus* sp.							X						61
	Trichiurus lepturus	X	X	X	X	X	X	X	X	X	X	X	X	40,41,56,59,61,63,68
Scombridae	*Acanthocybium solanderi*				X	X	X	X	X	X				2,25
	Auxis spp.	X	X	X	X	*	*	*	*	*	X	X		2,21,23,25,32,40,59,61, 63,64,68,79
	Euthynnus alletteratus				X	*	*	*	*	*	X	X		2,21,23,25,32,40,53,57, 59,61–64,68,79
	E. pelamis				X	X	X	X	X	X	X			2,21,23,25,32,40,61,63, 64,79
	Sarda sarda							X						53
	Scomber japonicus	X	X	X	X	X	X			X	X	X		2,32,40,61,63,68
	Scomberomorous cavalla					X	X	X	*	*	X	X		2,21,23,25,27,32,40, 50–52,59,61–65,68
	S. maculatus				X	X	X	X	*	*	X			2,23,25,27,32,40,50–53, 56,57,59,61–63,65,66,68
	T. albacares				X	*	*	*	X	X				40,63
	T. atlanticus				X	*	*	*	X	X	X	X		2,21,23,25,32,40,61,63, 64,79
	T. thynnus				X	X	X							2,21,23,25,32,40,61,64, 68,76–78,80
Xiphiidae	*Xiphias gladius*	X	X	X	*	*	*	X	X	X	X	X	X	19,23,25,64,79
Istiophoridae	*Istiophorus* sp.				X	X	X	X	X					2,16,23,25,61–64
Stromateidae	*Ariomma* spp.	X	X	X	X	X	X	X	X			X	X	2,40,41,57,59
	Cubiceps pauciradiatus	X	X	X	X	X	X	X	X	X	X	X	X	2,40,41,59,61,63,64
	Hyperoglyphe bythites					X	X	X	X					36
	Nomeus gronovii	X	X											40,41
	Peprilus paru				X	X	*	*	*	X	X	X		2,32,38,40,41,53,56,57, 59,61–63,66
	P. burti	*	*	*	X	X	X	X	X	X	X	*	*	2,32,38,40,41,53,57,59, 61–64,66,68
	Psenes spp.		X						X			X		2
	P. cyanophrys					X								2

TABLE 1.—*Continued.*

Family	Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Source
	P. pellucidus	X	X							X	X	X		2
	Tetragonurus atlanticus	X												59
Scorpaenidae	*Scorpaena* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,40,41,53,56,57,61–63, 66,68
Triglidae	*Peristedion* spp.					X								2
	Prionotus spp.	X	X	X	X	X	X	X	X	X	X	X	X	1–3,40,41,46,53,56–59, 61–64,66,68,69
Dactylopteridae	*Dactylopterus volitans*					X								2,40
Bothidae	*Bothus* spp.	X			X	X	X	X	X	X	X	X	X	32,40,41,45,59,61–64,68
	B. ocellatus	X	X	*	*	*	X	X	X	X	X	X	X	61–63,68
	B. robinsi		X	X	X	*	*	*	*	*	*	*		2,9
	Citharichthys spp.	X	X	X	X	X	X	X	X	X	X	X	X	32,40,46,56–59,63,66,68, 69
	C. cornutus	X	X		X	*	*	*	*	X	X	X		2,9,32,40
	C. gymnorhinus	X	X			X	X	X	X	X	X	X	X	2,9,32,40,59
	C. macrops	X	X	X	X	*	X	X	X	X	X	X		2,9,26
	C. spilopterus	X	X	X	X	X		X	X	X	X	X	X	2,26,40,41,45,53,59
	Cyclopsetta spp.	X	X	X		X	X	*	*	*	X	X		32,40,41,45,61–63,68
	C. fimbriata	X	X			X	*	X	X	*	X	X		2,9,62,63
	Engyophrys senta					X	X	X	X	X	X			2,20,32,40,41,45,53,59
	Etropus crossotus				X	X	X	X	X	X	X	X		26,32,40,41,45,46,56,57, 59
	E. rimosus	*	*	*	*	X	X	X	X	X	X	*	*	2,9,26
	Monolene sessilicauda					X	X	X	X	X	X	X	X	2,9,13,32,40,61,62,68
	Paralichthys spp.	*	*	X	X					X	X	X	*	1,2,40,41,45–47, 53,57, 59,61–63,66,68–70
	Syacium spp.				X	X	*	*	*	X	X	X	X	32,40,41,45,53,59,61–64, 68
	S. gunteri						X	*	*	X	X	X	X	32,40,57,61–63,66
	S. papillosum					X	*	*	*	*	X	X		2,9,14,32,40
	Trichopsetta ventralis					X	X	X	X	X	X			2,9,15,32,40,45
Soleidae	*Achirus lineatus*		X	X	X	X	*	*	*	X	X	X		2,3,40,41,45–47,53,56, 57,59,75
	Gymnachirus sp.				X	*	*	X						61,63
	G. melas		X			X	X					X		2
	Trinectes maculatus				X	X	*	X	X	X				1,40,46,53,58,66
Cynoglossidae	*Symphurus* spp.	X	X	X	X	X	X	X	X	X	X	X	X	2,3,40,45–47,53,56–59, 61–64,66,68,69
Balistidae	*Balistes* sp.							X	X					61
	Monacanthus sp.					X				X	X			61,62,68
	M. hispidus					X	X	X		X		X		46,53,69
	M. setifer											X		40
Ostraciidae	*Lactophrys* sp.					X	X						X	66,68
Tetraodontidae	*Lagocephalus laevigatus*					X				X				68
	Sphoeroides spp.	X	X	X	X	X	X	X	X	X	X	X	X	1,2,40,41,46,53,56,57, 59,61–64,66,68,69
Molidae	*Ranzania laevis*										X			64

[1]Blanchet 1979.
[2]Houde et al. 1979.
[3]Phillips et al. 1977.
[4]Houde 1981.
[5]Houde and Fore 1973.
[6]Smith 1980.
[7]Houde 1982.
[8]Leak 1981.
[9]Dowd 1978.
[10]Aprieto 1974.
[11]Caldwell 1957.
[12]Houde 1973.
[13]Futch 1971.
[14]Futch and Hoff 1971.
[15]Futch 1977.
[16]Gehringer 1957.
[17]Gibbs and Collette 1959.
[18]Gordon 1982.
[19]Grall et al. 1983.
[20]Hensley 1977.
[21]Juarez 1976.
[22]Houde 1976.
[23]Kelley et al. 1986.
[24]Montollo 1976.
[25]Richards et al. 1984.
[26]Tucker 1978.
[27]Dwinell and Futch 1973.
[28]Peters and McMichael 1987.
[29]Houde 1977a.
[30]Houde 1977b.
[31]Houde 1977c.
[32]SEAMAP 1983.
[33]Christmas and Waller 1975.
[34]Cowan 1985.
[35]Daniels 1977.
[36]Dawson 1971a.
[37]Dawson 1971b.
[38]Ditty 1981.
[39]Ditty 1984.
[40]Ditty 1986.
[41]Ditty and Truesdale 1984.
[42]Fore 1970.
[43]Fore 1971.
[44]Fruge 1977.
[45]Kuhn 1979.
[46]Ruple 1984.
[47]Sabins 1973.
[48]SEAMAP 1985.
[49]Shaw et al. 1985.
[50]Shaw and Drullinger 1985.
[51]Shaw and Drullinger 1986.
[52]Shaw et al. 1987.
[53]Stuck and Perry 1982.
[54]Thompson and Deegan 1982.
[55]Turner 1969.
[56]Vecchione et al. 1982.
[57]Walker 1978.
[58]Williams 1983.
[59]LDWF 1983 unpubl. data.
[60]SEAMAP 1984.
[61]Finucane et al. 1977.
[62]Finucane et al. 1979a.
[63]Finucane et al. 1979b.
[64]McGowan 1985.
[65]McEachran et al. 1980.
[66]Hoese 1965.
[67]Barger et al. 1980.
[68]Finucane 1976.
[69]Allshouse 1983.
[70]King 1971.
[71]Guillen and Landry 1981.
[72]Pearson 1929.
[73]Collins et al. 1980.
[74]Sogard et al. 1987.
[75]Houde et al. (1970, cited in Phillips et al. 1977).
[76]Richards 1976.
[77]Richards 1977.
[78]Richards and Potthoff 1980a.
[79]Richards and Potthoff 1980b.
[80]McGowan and Richards 1986.

TABLE 2.—Primary depth distribution of larvae (<10 mm SL) of some abundant taxa of fishes from the northern Gulf of Mexico above lat. 26°00'N. Depths are those reported in the literature at which >75% of larvae were collected. Asterisk (*) indicates larvae are estuarine-dependent.

Taxa	Depth (m)					Source
	<25	<50	<100	50–200	>150	
Chloroscombrus chrysurus	X					1,2,3,4,5,6,8,10
Orthopristis chrysoptera	X					1
Cynoscion nebulosus *	X					1,9,10
C. arenarius	X					1,2,9,10,11
Pogonias cromis *	X					11
Archosargus probatocephalus *	X					1
Chaetodipterus faber	X					2
Peprilus paru	X					1,25,26
Anchoa spp.		X				1
Harengula jaguana		X				1,4,5,6,13
Opisthonema oglinum		X				1,4,5,6,10,29
Brevoortia patronus *		X				14,15,16,17,32
Sardinella aurita		X				1,4,6,18
Diplectrum formosum		X				1
Serraniculus pumilio		X				1
Centropristis striata		X				1
Lagodon rhomboides *		X				1
Leiostomus xanthurus *		X				1,11,19,32
Micropogonias undulatus *		X				1,11,19,20,32
Scomberomorus maculatus		X				1,4,21,22,23,24
Decapterus punctatus			X			1,3,4,6
Peprilus burti			X			25,26
Etrumeus teres				X		1,5,6,11,12,27,28,30
Caranx crysos				X		1,3,4,6
Trachurus lathami				X		1,2,3,5,30
Hemanthias vivanus				X		1
Auxis sp.				X		1,21,22,23
Euthynnus alletteratus				X		1,21,22,30
Scomberomorus cavalla				X		20,23,24
Lutjanus campechanus				X		31
Xiphias gladius					X	7,21,22
Istiophorus spp.					X	21,22
Euthynnus pelamis					X	1,21,22,23

[1]Houde et al. 1979.
[2]Ditty and Truesdale 1984.
[3]Leak 1981.
[4]Shaw et al. 1987.
[5]Shaw and Drullinger 1986.
[6]Shaw and Drullinger 1985.
[7]Grall et al. 1983.
[8]Montolio 1976.
[9]Daniels 1978.
[10]Walker 1978.
[11]Cowan 1985.
[12]Houde 1977b.
[13]Houde 1977c.
[14]Shaw et al. 1985.
[15]Fore 1970.
[16]Turner 1969.
[17]Christmas and Waller 1975.
[18]Houde 1976.
[19]Fruge 1977.
[20]Finucane et al. 1977.
[21]Richards et al. 1984.
[22]Kelley et al. 1986.
[23]Dwinell and Futch 1973.
[24]McEachran et al. 1980.
[25]Ditty 1981.
[26]SEAMAP 1983.
[27]Fore 1971.
[28]Houde 1973.
[29]Houde 1977a
[30]Finucane et al. 1979b.
[31]Collins et al. 1980.
[32]Sogard et al. 1987.
[33]Richards and Potthoff 1980b.

crepancy in Spanish sardine seasonal occurrence reported by Houde and Fore (1973) (September–February) and that found by Shaw and Drullinger (1985, 1986), Shaw et al. (1987), and this review (March–November). Finally, seasonality data reported in Ditty (1986) for larvae of finescale menhaden, *Brevoortia gunteri*, was based on specimens subsequently believed to be a morph of gulf menhaden (*B. patronus*).

In general, the seasonal occurrence of many taxa of larval fishes (i.e., scaled sardine, *Harengula jaguana*, and Atlantic thread herring, *Opisthonema oglinum*) began both earlier and extended later in studies conducted on the Florida continental shelf and southern parts of the study area than those in the northern-most GOMEX. Likewise, in studies involving bays (e.g., Phillips et al. 1977; Blanchet 1979; Williams 1983), tidal passes (e.g., King 1971; Sabins 1973; Allshouse 1983), and barrier islands (e.g., Guillen and Landry 1981; Ruple 1984), peak seasonal occurrence of larvae of some fishes was usually later than in studies conducted offshore, primarily because of the time delay necessary for shoreward migration of estuarine-dependent larvae such as Atlantic croaker (*Micropogonias undulatus*), striped mullet (*Mugil cephalus*), pinfish (*Lagodon*

TABLE 3.—Location and sampling characteristics for northern Gulf of Mexico (GOMEX) ichthyoplankton studies. For months sampled: Q = quarterly, M = monthly, S = synoptic, B = biweekly. Numbers in columns with asterisk (*) refer to footnotes. Numbers separated by semicolons refer to specific gear types.

Study	Gear type*	Mesh size (mm)	Station depths (m)	Months/freq. sampled*	Study type/ taxa studied	Tow type*	Study location
Phillips et al. 1977	2	0.363	<10	10, B	Survey	13	Tampa/Hillsborough Bay, FL
Blanchet 1979	2	0.505	2–6	11, M	Survey	14	Lower Apalachicola Bay, FL
Houde et al. 1979	1, 2	0.505	10–200	9, Q	Survey	13	Florida continental shelf
Turner 1969	4	0.571	<58	9, Oct.–Apr.	*Brevoortia*	15, 19	Eastern and central GOMEX
Williams 1983	5	0.505	<10	11, M	Survey	14, 17	Lower Mobile Bay, AL
Struck and Perry 1982	2	1.050	10	9, M	Survey	14, 17	Off Mississippi Sound
Ruple 1984	4; 6	0.505, 0.571	4–7; 0.5	12, M	Survey	14, 19; 21	Horn Island, MS
Juarez 1976	2	0.505	>183	Q, Apr.–Nov.	Scombrids	13	Central GOMEX
Montolio 1976	2	0.505	>183	Q, Apr.–Nov.	Carangids	13	Central and western GOMEX
Fore 1971	—	—	27–108	M, Dec.–Apr.	*Etrumeus*	—	Central GOMEX
Sabins 1973	8	0.480	<1.5	11, M	Survey	19, 21	Caminada Pass, LA
Fruge 1977	1, 2	0.505	<91	Nov.	*Micropogonias*	13	Mississippi River Delta to Atchafalaya Bay, LA
Kuhn 1979	1	0.505	10–91	Nov., Jan., July	Bothids	13	Mississippi River Delta to Atchafalaya Bay, LA
Ditty and Truesdale 1984	1	0.505	10–91	Jan., July	Survey	13	Mississippi River Delta to Atchafalaya Bay, LA
Walker 1978	2	0.505	10–45	July, Aug., Dec.	Survey	15, 19	Mississippi River Delta to Timballer Bay, LA
Ditty 1986	1; 2	0.363	10; 30	11, M; 9, Q	Survey	14, 16, 17; 14	Off Caminada Pass, LA
Vecchione et al. 1982	1	0.333, 0.505	10	11, M	Survey	14, 16, 17	Southwest Louisiana off Calcasieu Lake
Cowan 1985	1	0.335	6–130	M, Dec.–Apr.	Sciaenids	18	Southwest Louisiana
Shaw et al. 1985	1	0.335	6–130	M, Dec.–Apr.	*Brevoortia*	18	Southwest Louisiana
Guillen and Landry 1981	8	1.000	<1.5	M, Jan.–Aug.	Survey	19, 21	Galveston Island, TX
McGowan 1985	1	0.333	Over reef	9, Q	Survey	13, 20	Flower Gardens Reef, TX
King 1971	4	1.000	<5	9, M	Survey	14, 16, 17	Cedar Bayou Pass, TX
Hoese 1965	2	0.086	6–50	9, M	Survey	14	Off Port Aransas, TX
Allshouse 1983	4	0.505	3–12	11, M	Survey	13	Aransas Pass, TX
Finucane 1976	2	0.250	18–135	Dec., Apr., Aug.	Survey	13	South Texas continental shelf
Finucane et al. 1977, 1979b	1	0.333, 0.505	18–182	9, M	Survey	13	South Texas continental shelf
Finucane et al. 1979a	1	0.333, 0.505	17	July, Oct., Feb.	Survey	13	Off Galveston, TX
Fore 1970	7	—	7–75	M, Sept.–Apr.	*Brevoortia*	18	Central and western GOMEX
Christmas and Waller 1975	2; 4	0.505; 1.000	2–110	9, Oct.–Apr.	*Brevoortia*	13; 14	Gulf-wide
Richards and Potthoff 1980a, b	1; 3	0.505; 0.946	>183	9, Apr.–May	Scombrids	13; 14	Gulf-wide
SEAMAP 1983–1985	1; 3	0.333; 0.946	>10	9, S	Survey	13; 14	Gulf-wide

[1]60 cm bongo.
[2]1 m met.
[3]1 × 2 m neuston.
[4]0.5 m net.
[5]1 × 0.5 net.
[6]2 × 0.5 m.
[7]Gulf-V sampler.
[8]Renfro beam trawl.
[9]Multiyear.
[10]15 months.
[11]12 months.
[12]14 months.
[13]Oblique.
[14]Surface.
[15]Subsurface.
[16]Middepth.
[17]Bottom.
[18]Stepwise oblique.
[19]Horizontal.
[20]Oblique at select depth intervals.
[21]Surf zone.

rhomboides), black drum, red drum, and gulf menhaden.

The seasonal occurrence of several taxa are known only from a few scattered specimens (e.g., cornetfish, *Fistularia* sp.; ribbonfish, *Trachipterus* sp.; cowfish, *Lactophrys* sp.; slender mola, *Ranzania laevis*; threadfish, *Polydactylus* sp.; and cobia, *Rachycentron canadum*) or a single monthly record (Table 1). Larvae of other taxa (e.g., searobins, *Prionotus* spp.; anchovies, *Anchoa* spp.; tonguefishes, *Symphurus* spp.; and pufferfishes, *Sphoeroides* spp.) were collected during all months (Table 1), reflecting the many species that comprise each genus. In general, larvae of most scombrids were collected beyond the 50 m depth contour, except Spanish mackerel, *Scomberomorus maculatus*, which occurred primarily within 50 m. Finucane et al. (1979b) collected 50% of their king mackerel, *S. cavalla*, larvae off Texas during September and found this species relatively more abundant and over greater water depths (35–183 m) than Spanish mackerel (<35 m). In the north-central GOMEX, larvae of

Spanish mackerel were more abundant than those of king mackerel, and spawning of this latter species probably occurs over shallower depths than in the northwestern GOMEX (Shaw et al. 1987). Only six larvae of king mackerel were collected by Houde et al. (1979), suggesting that this species does not use the northeastern GOMEX as a major spawning area. Larvae of cero, *S. regalis*, have not been reported from the study area. Larvae of sciaenids and engraulids occurred primarily within the 50 m depth contour, with several species of sciaenids primarily collected inside the 25 m contour (Table 2). Both sciaenids and engraulids are relatively more abundant in the north-central and northwestern than in the northeastern GOMEX (Finucane et al. 1977, 1979b; Houde et al. 1979; Richards et al. 1984; Kelley et al. 1986) (Table 4). Most larvae of clupeids occur in shelf waters of <50 m depth, except those of round herring, *Etrumeus teres*, which primarily occur beyond the 50 m contour (Table 2). Larvae of gulf menhaden are more abundant in the north-central than either the northeastern or northwestern GOMEX and occur primarily around the Mississippi River Delta (Fore 1970; Christmas and Waller 1975; Sogard et al. 1987; and others). Scaled sardine and Atlantic thread herring larvae are abundant in all three subregions of the northern GOMEX; Spanish sardine are rare in the north-central but relatively abundant in the northeastern and northwestern GOMEX (Shaw and Drullinger 1985, 1986; Shaw et al. 1987). Larvae of gulf butterfish, *Peprilus burti*, and harvestfish, *P. paru*, are most common in the north-central GOMEX (SEAMAP 1983), with only a few of their larvae (8 and 25, respectively) having been collected by Houde et al. (1979) in the northeastern GOMEX. Although gulf butterfish larvae have been collected during every month (Table 1), larvae are most common from November to March with very limited spawning during the summer (Ditty 1981; SEAMAP 1983). Houde et al. (1979) also collected >90% of both sparid and haemulid larvae inside the 50 m contour during their Florida continental shelf survey and found that although lutjanids occurred at all depths, they were most abundant from 30 to 100 m. Unlike larvae of other speciose families which primarily occurred either within (e.g., clupeids, engraulids, and sciaenids) or beyond (e.g., scombrids) the 50 m depth contour, those of bothids, carangids, and serranids were widely distributed and occurred at all depths. Larvae of swordfish, *Xiphias gladius*, and sailfish, *Istiophorus* sp., are oceanic and occurred primarily outside the 200 m depth contour; leptocephali of tarpon, *Megalops atlanticus*, and bonefish, *Albula vulpes*, were seldom collected in the study area. Of those taxa whose larvae were most abundant within the 25 m contour (Table 2), several were most commonly collected at considerably shallower depths (e.g., pigfish, *Orthopristis chrysoptera* <20 m; black drum <18 m; and spotted seatrout, *Cynoscion nebulosus* <15 m). Larvae of other taxa which occurred primarily within the 25 m contour includes leatherjacket, *Oligoplites saurus* (<20 m; Houde et al. 1979); kingfish, *Menticirrhus* spp. (<20 m; Walker 1978; Houde et al. 1979; Cowan 1985); and spottail pinfish, *Diplodus holbrooki* (<15 m; Houde et al. 1979). Larvae of hogchoker, *Trinectes maculatus*, and silver perch, *Bairdiella chrysoura*, were occasionally collected in neritic offshore studies, but were most abundant in pass/estuarine studies (e.g., Sabins 1973; Allshouse 1983).

TABLE 4.—Comparison of 10 most abundant families of larval fishes collected during major ichthyoplankton surveys of the Gulf of Mexico. Rank is based on number of individuals collected. Numbers are % of total collection.

Taxa	Finucane 1976	Finucane et al. 1977	Finucane et al. 1979b	Houde et al. 1979	Kelley et al. 1986
Engraulidae	17.4	13.5	6.2		14.6
Gobiidae	16.6	20.6	15.8	15.1	6.2
Bregmacerotidae	14.5	12.5	7.3	2.7	5.4
Clupeidae	8.5	5.0	8.1	20.5	9.6
Sciaenidae	5.3	2.1			3.1
Carangidae	4.8	3.1	3.7	3.9	4.1
Bothidae	4.6	8.4	6.1	6.4	4.4
Synodontidae	4.5	3.6	10.9	3.0	
Myctophidae	3.0	5.0	4.9	5.1	11.2
Serranidae	2.0		2.2	4.9	
Cynoglossidae			3.4		
Scombridae		1.9			
Ophidiidae				2.9	
Labridae				2.3	
Gonostomatidae					3.3
Mugilidae					2.5
Totals	81.2	75.7	68.6	66.8	64.4

In conclusion, these data represent the current knowledge of the seasonality, peak occurrence, and primary depth distribution of larval fishes in the northern GOMEX. This information provides a foundation upon which sound management decisions concerning both the commercial and recreational exploitation of spawning aggregations of fishes and the potentially adverse impact on these fisheries resulting from such exploitation can be based.

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UTILIZATION OF A WASHINGTON ESTUARY BY JUVENILE ENGLISH SOLE, *PAROPHRYS VETULUS*

The use of west coast estuaries and protected bays as nursery grounds by English sole, *Parophrys vetulus* Girard, a significant component of Pacific coast groundfish landings, has been well documented (Westerheim 1955; Kendall 1966; Smith and Nitsos 1969; Misitano 1970). From data collected off Oregon, Laroche and Holton (1979) showed that English sole also utilize nearshore areas along the open coast as nursery grounds. Krygier and Pearcy (1986) determined that estuarine dependence for juvenile English sole was indeed significant relative to the open coastal area off Oregon, although their survey design made it difficult to compare absolute abundance in these areas. In addition, the estuaries studied by Krygier and Pearcy were much smaller than the Washington estuaries of Grays Harbor and Willapa Bay, making it difficult to extrapolate their results.

In the present study our objectives were to 1) compare relative density and estimates of abundance of 0-age English sole between a Washington estuary, Grays Harbor, and the adjacent area along the open coast; 2) compare fish density between several subareas (strata) of each system; and 3) note timing of immigration to and emigration from the estuary. Specific gear was developed to efficiently sample small benthic organisms and was used in both the estuary and open coast survey areas, eliminating the need for gear selectivity intercalibration. In addition, the statistical design of the survey enabled population estimates with confidence intervals to be made for each area.

Methods and Materials

Survey Design

For this study, we specifically developed a plumb staff beam trawl with an effective width of 2.3 m. We designed it for a quantitative assessment of juvenile fishes and crustaceans closely associated with the bottom. Its fine mesh (4 mm) cod end liner retained newly settled flatfish (15–25 mm total length). A complete account of its construction, method of deployment, and field testing was given by Gunderson and Ellis (1986).

We selected two separate survey areas for the study, the Grays Harbor estuary and the adjacent nearshore area along the open coast. The estuarine survey was based on a stratified random statistical design and the open coast survey on a systematic trackline. Both areas were surveyed in 1983 and 1984.

The estuary was stratified into four geographic areas (Fig. 1). Each stratum was divided into 1 × 1 km grids (1 km intervals in the case of narrow channels), and several stations were then randomly selected with the constraint that no two be adjacent. Additional stations were added in both STR (stratum) 1 and 2 for the 1984 survey.

For the open coastal survey, three tracklines oriented perpendicular to the bathymetry were located off Copalis Head, Westport, and Willapa Bay (Cape Shoalwater) (Fig. 2). We established a systematic series of stations along each trackline at 9 m depth intervals from 9 to 64 m. Whenever wave conditions permitted, we sampled an additional station at 5.5 m. In 1984, the 64 m stations were dropped on each trackline because of consistent gear damage in 1983. Also in 1984, replicate tows were made at the 27 and 37 m stations.

Sampling Schedule

We sampled the estuary twice monthly from April through September 1983 and 1984, and a single trip was made in January 1984 for continuity. The two

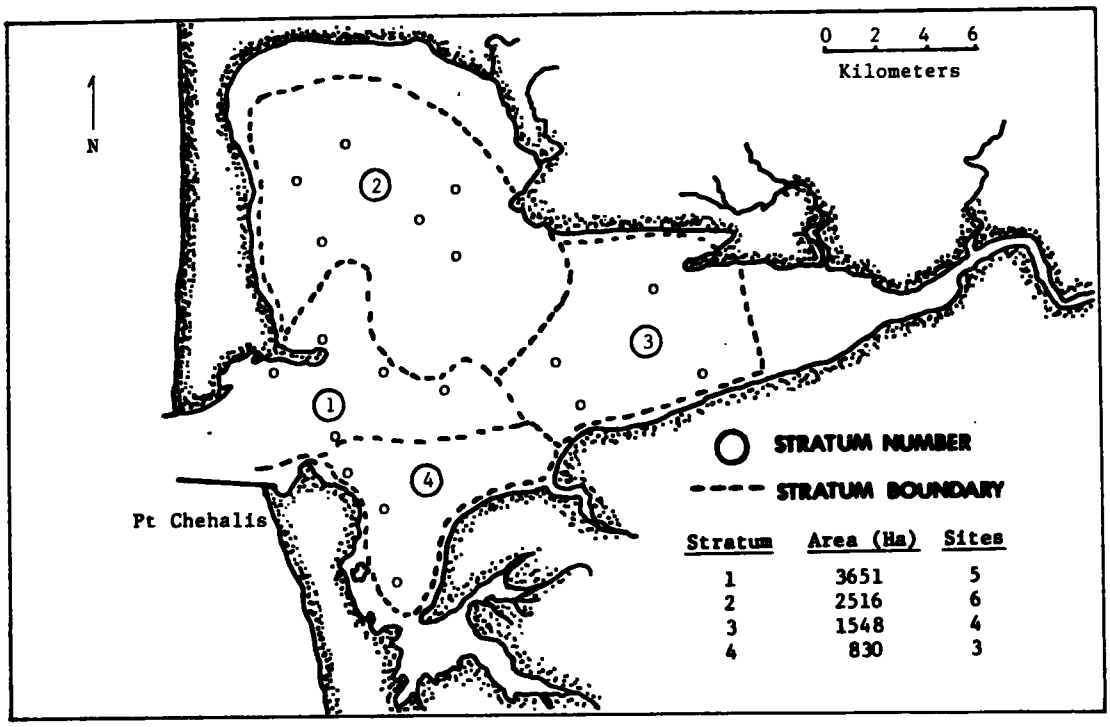

FIGURE 1.—Chart of Grays Harbor, WA, showing the four strata and random trawl sites selected from grid lines.

trips per month coincided with low tides when navigation and location of stations within the narrow channels characteristic of the North Bay and Inner Harbor would be easiest. Stations situated in the shallow, unmarked channels were sampled at low water, while stations in more navigable areas were sampled during the following periods of high water. All hauls were confined to slack tide periods so that strong tidal currents would not interfere with the operation of the beam trawl. We sampled the offshore study area once a month from April through September.

Field Techniques

Within the estuary, the plumb staff beam trawl was operated from a 6 m outboard boat, while offshore, either a 17 m or 20 m vessel was chartered. Mechanical or hydraulic winches allowed the retrieval of the beam trawl while underway, reducing escapement of captured organisms from the net.

At all stations, the beam trawl was hauled for a distance dependent on the amount of epibenthic material expected. Hauls of <10 minutes duration (200–300 m) were necessary within the estuary because the small mesh cod end liner would clog with mud and organic debris, making the net difficult to retrieve. Although the same problem existed in the open coast survey area, hydraulic lifting gear enabled hauls of up to 20–30 min duration (800–1,000 m) at most stations. We attempted to tow at 3 km/h with a scope of about 5:1; at depths <5 m, the scope was increased to 10:1.

Within the estuary, marker buoys were deployed where we estimated the trawl started and stopped fishing. The distance fished was determined by measuring between buoys with an optical rangefinder. Along the open coast, Loran C readings were recorded at points we estimated the trawl first contacted and left bottom and were later converted to distance fished.

We sorted most of the catch by species (some fishes to family only), and information was recorded for total weight and number per haul. Random subsampling of the catch (never <20% by weight) was performed when necessary to speed processing. Length frequencies and individual lengths and weights were recorded for selected species.

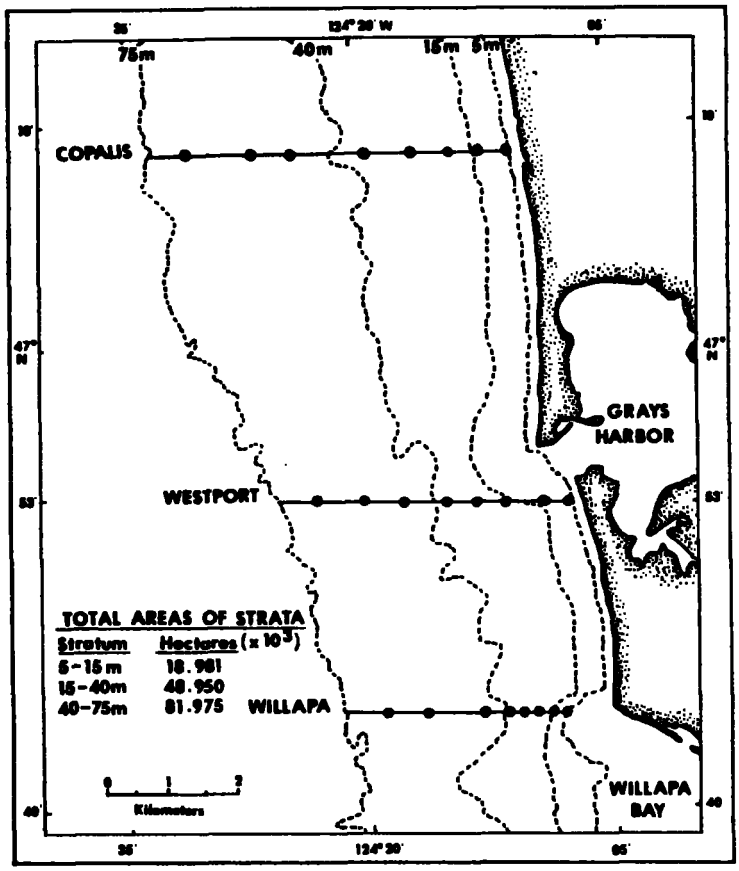

FIGURE 2.—Chart of the open coast adjacent to Grays Harbor, WA, showing the isobaths, tracklines, and systematic trawl stations.

Data Analyses

Nautical charts of Grays Harbor and the adjacent open coast were digitized and strata areas were calculated (Figs. 1, 2), using computerized algorithms available in the software library of the NWAFC Resource Assessment and Conservation Engineering Division. Strata were defined for the offshore area by first extending the north and south boundaries 5 nmi from the Copalis and Willapa transects, respectively, and then determining the area between the 5, 15, 40, and 75 m depth contours.

Estimates of mean density of young English sole by stratum by month, population by stratum, and total population for each survey area were calculated, using slight modifications of the methods of Pereyra et al. (1976). In calculating density estimates (number/hectare) from catch per kilometer, the efficiency coefficient of the gear was assumed to be unity (i.e., all fishes in the path would be captured). Length frequencies for 5 mm (TL) size intervals were used to calculate size composition. Age classes were then determined by visual inspection of the resultant length-frequency histograms. Afterwards, the proportion of individuals within the size range of the 0-age group in a particular month was multiplied by the total population for that month to provide an estimate of the abundance of 0-age recruits.

Results

Over the course of the 2-yr study, we completed a total of 592 trawls, 349 within Grays Harbor and 243 along the open coast (Table 1). Hauls within the

TABLE 1.—Allocation of sampling effort indicating the number of successful trawls completed for each trip.

Survey area	1983			1984		
	Month	Trips	Trawls	Month	Trips	Trawls
Estuary	Apr.	2	9,13	Jan.	1	13
	May	2	13,16	Apr.	1	5
	June	2	16,14	May	2	15,16
	July	2	16,16	June	2	18,18
	Aug.	2	14,16	July	2	18,17
	Sept.	1	16	Aug.	2	19,17
	Oct.	1	16	Sept.	1	18
Total			175			174
Open coast	May	1	17	Apr.	1	19
	July	1	20	May	1	23
	Aug.	1	25	June	1	26
	Sept.	1	48	Aug.	1	32
				Sept.	1	33
Total			110			133

estuary averaged 0.25 km at 2.52 km/h, while in the coastal study area they averaged 0.91 km at 3.32 km/h.

Distribution and Abundance

We captured a total of 13 species of flatfishes in the two study areas during the 2-yr survey (Table 2). Juvenile sanddab, sand sole, and English sole were found to be abundant both in Grays Harbor estuary and along the open coast. Two species in particular, English sole and starry flounder, were found to have much higher densities in the estuary than along the open coast (Table 2). English sole were found to be the most abundant flatfish in the estuary for both years and along the open coast in 1984.

For both years within Grays Harbor, densities of English sole generally were highest in STR 1, 2, and 4 and lowest densities in STR 3 (Table 3). Apart from changes due to recruitment, fluctuation in abundance in the four areas of the estuary was likely affected by movement of juveniles between strata and between the estuary and open coast. Along the open coast, greatest densities were observed nearshore (Table 4) in depths <40 m. In 1984, English sole were most abundant at 5–15 m owing to the presence of high numbers of 0-age fish.

Mean density (all months combined) within the estuary was over 20 times greater than the open coast in 1983. Settlement of fish <25 mm TL was much greater in 1984 than 1983 in both areas, but estuarine density was still higher than that of the open coast. A *t*-test was performed on log-transformed CPUE (Zar 1984) because catch data are typically nonnormally distributed. Results showed a significantly greater density ($P < 0.0001$) of juvenile English sole in the estuary than along the open coast for both 1983 (562 vs. 23 mean no./ha) and 1984 (1,149 vs. 178 mean no./ha).

Population Estimates

In making population estimates, mean densities of fish less than age V by month were multiplied by strata areas. Comparison of length frequencies of fish we collected with published age-at-length relationships (Van Cleve and El Sayed 1969) indicated that fish beyond age IV were rarely captured. Older fish may not have been present in the study areas

TABLE 2.—Stratified mean densities and 2 SE (in parentheses) for juvenile flatfish captured in the two survey areas for 1983–84.

Species	1983 densities (no./ha)		1984 densities (no./ha)	
	Estuary	Open coast	Estuary	Open coast
English sole, *Parophrys vetulus*	562(132)	23(10)	1,149(237)	178(101)
Pac. Sanddab, *Citharichthys sordidus*	147(30)	94(24)	94(33)	65(22)
Butter sole, *Isopesetta isolepsis*	<1	37(10)	<1	13(4)
Sand sole, *Psettichthys melanosticus*	27(11)	10(6)	36(14)	23(11)
Dover sole, *Microstomus pacificus*	—	11(5)	—	8(4)
Rex sole, *Glyptocephalus zachirus*	—	10(5)	—	2(2)
Slender sole, *Lyopsetta exilis*	—	2	—	1
Starry flounder, *Platichthys stellatus*	25(16)	<1	10(7)	1
Petrale sole, *Eopsetta jordani*	—	<1	—	<1
Rock sole, *Lepidopsetta bilineata*	—	<1	—	<1
C-O sole, *Pleuronichthys coenosus*	<1	<1	—	—
Curlfin sole, *Pleuronichthys coenosus*	<1	<1	—	<1
Cal. tonguefish,[1] *Symphurus atricauda*	<1	<1	—	—

[1]Occurrence considered anomolous (Dinnel and Rogers 1986).

TABLE 3.—Population estimates for juvenile English sole in the estuary survey area by date (month/year) and by stratum (1–4). The 95% confidence interval for the total population is obtained by adding or substracting the value in parentheses.

Date	Stratum	Density (no./ha)	Population (millions)	Date	Stratum	Density (no./ha)	Population (millions)
4/83	1	82	0.301	1/84	1	66	0.239
	2	127	0.318		2	100	0.251
	3	312	0.483		3	207	0.320
	4	383	0.318		4	158	0.131
	Total		1.421 (0.851)		Total		0.942 (0.472)
5/83	1	1,138	4.154	5/84	1	2,191	7.999
	2	297	0.747		2	4,858	12.223
	3	84	0.130		3	575	0.890
	4	1,825	1.515		4	2,045	1.697
	Total		6.545 (5.045)		Total		22.808 (8.686)
6/83	1	681	2.488	6/84	1	1,092	3.986
	2	961	2.417		2	1,049	2.639
	3	71	0.110		3	160	0.248
	4	801	0.665		4	835	0.693
	Total		5.679 (3.089)		Total		7.565 (4.195)
7/83	1	717	2.616	7/84	1	1,360	4.966
	2	775	1.950		2	2,470	6.214
	3	222	0.344		3	212	0.328
	4	740	0.614		4	1,087	0.902
	Total		5.524 (3.836)		Total		12.411 (5.569)
8/83	1	648	2.365	8/84	1	1,285	4.691
	2	662	1.666		2	939	2.362
	3	390	0.604		3	417	0.645
	4	468	0.388		4	402	0.333
	Total		5.023 (2.898)		Total		8.031 (3.557)
9/83	1	765	2.793	9/84	1	124	0.451
	2	291	0.733		2	558	1.403
	3	195	0.301		3	755	1.169
	4	524	0.435		4	262	0.217
	Total		4.262 (2.772)		Total		3.241 (1.745)
10/83	1	125	0.457				
	2	598	1.505				
	3	564	0.873				
	4	115	0.095				
	Total		2.931 (1.251)				

or, more likely, were better able to avoid the narrow beam trawl.

Within the estuary, English sole were most numerous in May of both years, but the peak of 22.8 million in 1984 was more than 3 times higher than the peak of 6.5 million in 1983 (Table 3). Although the distribution of the English sole population within the estuary was highly variable, the bulk of the population was in STR 1 or STR 2 for most months. Along the open coast, the English sole population peaked at the same time and at generally the same levels as the estuary for both years, about 5.9 and 23.2 million for 1983 and 1984, respectively (Table 4). Comparable populations of young fish occurred in both areas despite the 18 times greater geographic extent of the offshore survey area.

Recruitment

Relative recruitment to the two survey areas was measured in terms of populations of 0-age fish. Within the estuarine study area, recently transformed (<25 mm TL; Laroche et al. 1982) English sole were observed from April to July in 1983, and in January and from May to August in 1984. Peak abundance of this size range was observed in May of both years, but it is highly likely that early spring peaks were missed since our study lacked adequate coverage of fall, winter, and early spring months. Duration of settlement along the Oregon coast is known to be much longer than observed in our study (Laroche and Richardson 1979; Boehlert and Mundy 1987). Along the open coast, settlement seemed to

TABLE 4.—Population estimates for juvenile English sole in the open coast survey area by date (month/year) and by stratum (1–4). The 95% confidence interval for total population is obtained by adding or substracting the value in parentheses.

Date	Depth (m)	Density (no./ha)	Population (millions)	Date	Depth (m)	Density (no./ha)	Population (millions)
5/83	5–15	6	0.115	4/84	5–15	165	3.124
	15–40	100	4.881		15–40	47	2.318
	40–75	11	0.887		40–75	55	4.525
	Total		5.883 (4.666)		Total		9.967 (7.071)
7/83	5–15	2	0.044	5/84	5–15	190	3.598
	15–40	20	0.983		15–40	80	3.911
	40–75	8	0.680		40–75	191	15.667
	Total		1.707 (1.840)		Total		23.176 (19.225)
8/83	5–15	54	1.028	6/84	5–15	226	4.282
	15–40	35	1.709		15–40	48	2.356
	40–75	12	0.991		40–75	9	0.732
	Total		3.728 (2.390)		Total		7.370 (3.110)
9/83	5–15	12	0.230	8/84	5–15	903	17.133
	15–40	32	1.547		15–40	14	0.670
	40–75	3	0.269		40–75	21	1.724
	Total		2.045 (0.902)		Total		19.527 (18.981)
				9/84	5–15	97	1.836
					15–40	322	15.761
					40–75	5	0.402
					Total		18.000 (11.494)

be of shorter duration, though again, the survey lacked sampling effort from October through March. Recently transformed juveniles were captured only during May in 1983 and were found from April to September in 1984. Peak abundance was observed in May as in the estuary.

Populations of 0-age fish were determined using estimates of total juvenile population (Tables 3, 4) and size-frequency data (Table 5). These estimates show that English sole had higher recruitment to the estuary than to the open coast for early spring of both years. The estuarine population of young-of-the-year exceeded that of the open coast by over four times (6.4 vs. 1.5 million) in May 1983. The difference was less pronounced in May 1984, but the estuarine population was again higher (22.8 vs. 19.0 million). Later in summer in both years, the estuarine population of 0-age fish declined to a greater extent than that along the open coast, but some of the relative change is likely due to emigration from the estuary.

Densities were plotted by 5 mm length interval for the estuarine and open coast study areas for May each year, a period of high settlement (Fig. 3). Densities of juveniles <25 mm were more than 10 times greater in the estuary, indicating disporportionately higher direct settlement and/or higher mortality of newly settled juveniles in the open coast area. When

TABLE 5.—Length ranges (mm TL) of 0-age English sole determined from visual inspection of length-frequency distributions by study area and by date (month/year). Modal and mean lengths, and the proportion of total population comprised by the 0-age group are also indicated.

Study area	Date	Range (mm)	Mode (mm)	Mean (mm)	Proportion
Estuary	4/83	19– 84	65	57.6	0.85
	5/83	19– 99	30	50.5	0.97
	6/83	18–114	40	62.5	0.98
	7/83	26–119	55	73.8	0.99
	8/83	43–124	70	79.1	0.99
	9/83	49–145	80	87.0	1.00
	10/83	62–130	85	92.8	1.00
	1/84	25– 54	35	34.9	0.58
	5/84	15– 84	20	26.9	1.00
	6/84	20– 99	30	46.4	0.96
	7/84	25–114	85	66.9	0.99
	8/84	30–124	90	84.8	0.99
	9/84	50–135	90	92.0	1.00
Open coast	5/83	21– 60	35	33.3	0.25
	7/83	99–115	100	104.0	0.07
	8/83	43–165	120	115.4	0.80
	9/83	53–200	110	134.7	0.89
	4/84	15– 35	20	19.5	0.90
	5/84	15– 90	20	26.5	0.82
	6/84	15–120	30	48.6	0.87
	8/84	20–160	95	91.0	0.98
	9/84	20–180	130	119.0	0.89

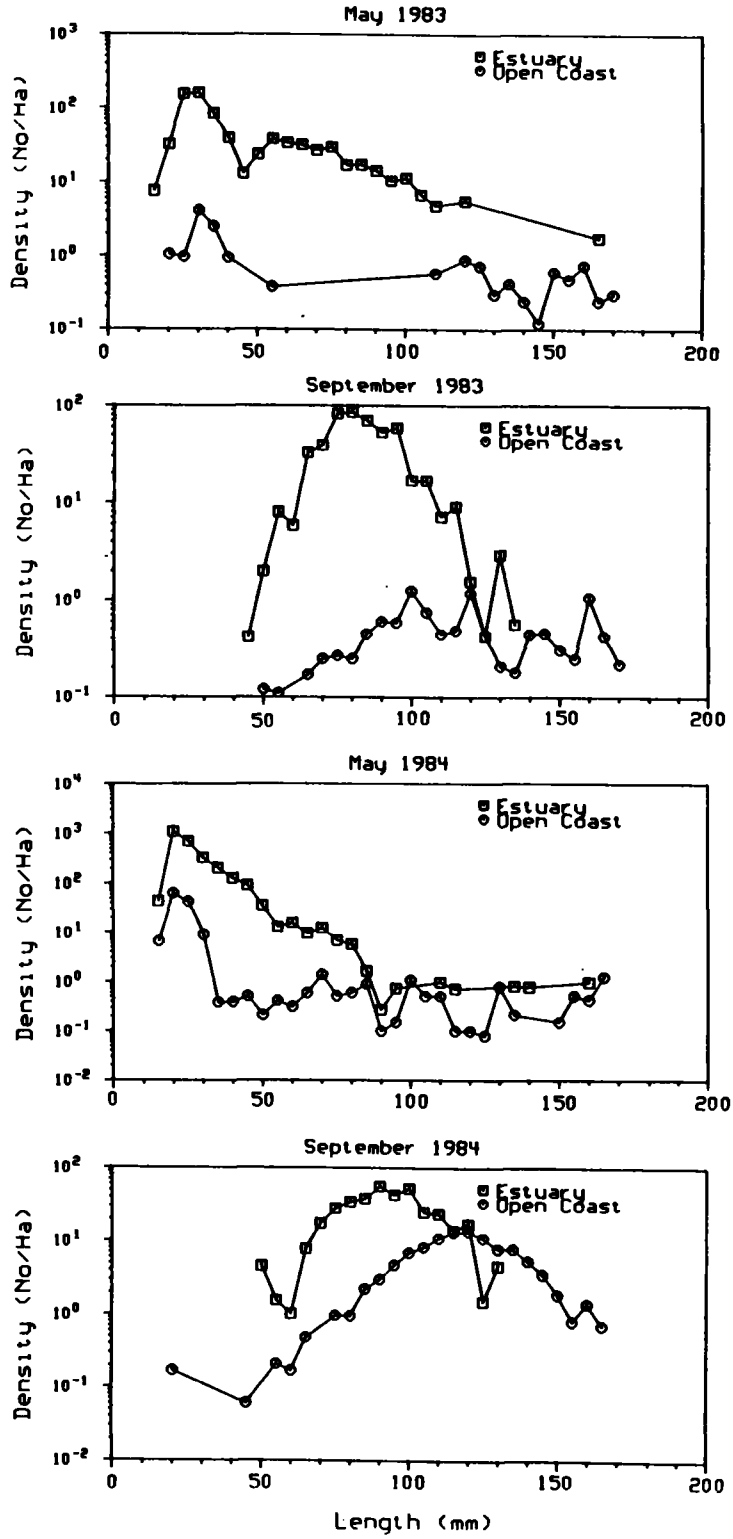

FIGURE 3.—Density of juvenile English sole by length interval for May and September of 1983 and 1984. Note the higher density of 0-age fish in the estuary each spring.

densities were plotted by length interval the following September of each year, it was evident that fish over 140 mm were not available in the estuary and had probably emigrated to the open coast.

Discussion

If there is an adaptive advantage in utilizing estuarine nursery grounds rather than the open coast, there must exist a mechanism for 0-age fish to enter estuarine systems. Although English sole larvae are abundant in coastal waters (Richardson and Pearcy 1977), early stages have not been prevalent in estuarine larval surveys (Pearcy and Meyers 1974; Misitano 1977). Large transforming larvae (18–23 mm) have been collected in Humboldt Bay and Columbia River estuary (Misitano 1976, 1977), and in Yaquina Bay (Boehlert and Mundy 1987). Immigration of 0-age English sole to the Grays Harbor estuary may be accomplished by direct settlement of transforming larvae after simple advection by ocean water into the bay, or by movements of newly settled benthic juveniles. Such movement could be accomplished either actively or by selective tidal transport as noted for juvenile flatfishes in the North Sea (DeVeen 1978).

During the period of this study, newly transformed English sole were found both within the Grays Harbor estuary and along the adjacent open coast. English sole have also been shown to enter Yaquina Bay after settlement (Boehlert and Mundy 1987) so it is likely that both transforming larvae and settled juvenile English sole may enter Grays Harbor. Krygier and Pearcy (1986) found newly transformed English sole to be more abundant in open coastal areas and presumed movement into Oregon estuaries to occur predominantly after transformation. The occurrence of recently transformed benthic juveniles in such high numbers throughout Grays Harbor suggests direct settlement of late stage larvae after advection into the estuary may also be an important mode of entry.

Emigration of the largest fish to the open coast took place during late summer, and all fish larger than 140 mm were found exclusively in the open coast area by September. Studies of other estuarine nursery areas have indicated that the emigration process involves the larger size classes of 0-age fish (Herke 1971; Weinstein 1983). Emigration from Yaquina Bay of the larger 0-age English sole has been noted in the fall (Westrheim 1955; Olsen and Pratt 1973; Bayer 1981). Angell et al. (1975) observed a similar phenomenon for young English sole in a Puget Sound nursery area.

The departure of larger juveniles later in summer may be in response to changing environmental conditions and may be indicative of the limits of the carrying capacity of estuaries being exceeded for populations of juvenile fish (Krygier and Pearcy 1986). Alternatively, a change in dietary preferences of larger 0-age fish may cause them to leave estuaries in search of prey items (Toole 1980), thus reducing intraspecific competition. The advantage in utilization of estuarine nurseries then, may be more for protection of vulnerable sizes rather than for accelerated growth (Rosenberg 1982).

Even though our study found a great deal of interannual variability, the Grays Harbor estuary and other nearby estuaries (Shi 1987) clearly are important nursery grounds for juvenile English sole, which had similar size populations in the estuarine and offshore study areas despite the greater geographic extent of the latter. Peak population estimates for 0-age English sole for the month of May show that 81% and 54% of 0-age fish in the Grays Harbor area were found in the estuary in 1983 and 1984, respectively. This is probably an underestimate of the degree of estuarine dependence, however, because some juveniles may move into the estuary later in the summer. Nevertheless, our results show that at least half of the 0-age English sole in the Grays Harbor nearshore area make use of an estuary during the first year of life. This kind of information will prove useful in assessing the economic impact on commercial fisheries from navigation and industrial development projects, which may contribute to habitat degradation in Grays Harbor.

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LENGTH-WEIGHT RELATIONSHIPS FOR GULF FLOUNDER, *PARALICHTHYS ALBIGUTTA*, FROM NORTH CAROLINA

Ginsburg (1952) resolved that the gulf flounder, *Paralichthys albigutta*, ranging from North Carolina to Laguna Madre, TX (Topp and Hoff 1972; Hoese and Moore 1977; Robins and Ray 1986), was a *Paralichthys*. Topp and Hoff (1972) summarized the many distributional records known throughout its range. Other than keys to the species of *Paralichthys* (Gutherz 1967), much of the biology of the gulf flounder remains unknown even though it abounds east of the Mobile Bay system (Joseph and Yerger 1956; Topp and Hoff, 1972; Shipp 1986).

Some researchers cite a 390 mm (total length, TL) Cedar Key, FL specimen (Jordan and Swain 1885) as the largest size attained by the gulf flounder (Hoese and Moore 1977; Robins et al. 1986). Vick (1964) noted a 710 mm, 5 kg, specimen in the sport fishery off Panama City, FL but did not furnish data on specimens larger than 380 mm TL.

We present length-weight regression data for North Carolina gulf flounder from 263 to 673 mm TL and 318 to 3,706 g.

Methods

Since 1975, 75 gulf flounder were speared while scuba diving along the Cape Lookout rock jetty (13 km east) and the artificial fishing reef (3 km SE) off Morehead City, NC. Most dives occurred in November and December, when *P. albigutta* and other paralichthids congregated in nearshore ocean waters off Carteret County, NC prior to their offshore spawning migration. Specimens were weighed to the nearest gram on beam balances and measured (total length) in millimeters within hours of capture.

Observations

While gulf flounder are not abundant in North Carolina (Schwartz et al. 1979, 1982), they are captured by hook and line or spear fishermen when the fish frequent high saline nearshore ocean waters or inlets (Schwartz 1979, 1982). Species of *Paralichthys* can usually be separated from each other by the number of gill rakers on the lower first gill arch, fin ray count, spotting, body width, salinity preference, and depth distribution preference (Gutherz 1967). Gulf flounder possess 9–12 (usually 10–11) gill rakers on the lower first arch, 53–63 anal rays, and three prominent ocellated spots arranged in a triangular pattern. North Carolina gulf flounder had 9–13 gill rakers on the lower first arch (65 specimens) and 54–67 anal fin rays. Complete anal rays were not counted in 17 specimens.

Gulf flounders caught consisted of 13 males and 62 females. Males ranged from 310 to 426 mm TL

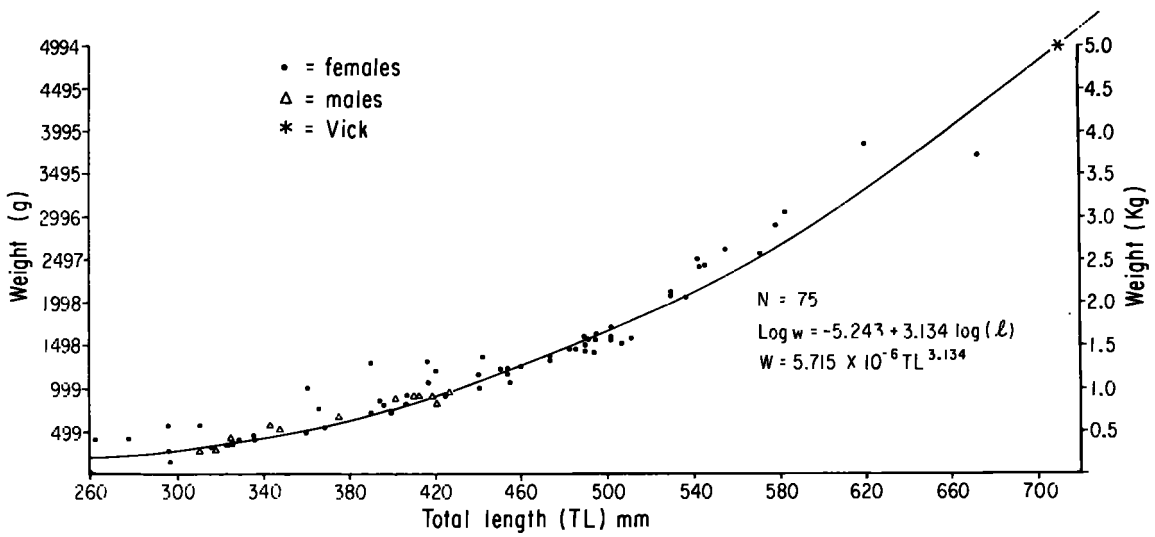

FIGURE 1.—Length-weight relationship for gulf flounders, *Paralichythys albigutta*, from North Carolina. Asterisk represents Vick's specimen.

and weighed 318 to 949 g, while females ranged from 263 to 673 mm TL and 408 to 3,706 g (Fig. 1). The length-weight relationship for North Carolina gulf flounder can best be expressed as $\log w = -5.24 + 3.134 \log l$ for 75 specimens (sexes combined), $r = 0.957$ (Fig. 1). Little change occurred when the male data was removed because the female length-weight relationship was virtually the same: $\log w = -5.018 + 3.053 \log l$ ($N = 62$), $r = 0.955$. Vick's (1964) large specimen, 710 mm TL, 5,000 g, fits right on our regression curve. Thus, there is little doubt that his specimen was *P. albigutta* because *P. dentatus* does not occur in the Gulf of Mexico (Robins and Ray 1986), and *P. squamilentus* or *P. lethostigma* possess other distinguishing meristic, morphometric, and ecological requirements (Vick 1964; Gutherz 1967).

The maximum known upper size and weight can now be raised to at least 673 mm and 3,706 g in North Carolina.

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FUNCTIONAL REGRESSION EQUATIONS FOR ZOOPLANKTON DISPLACEMENT VOLUME, WET WEIGHT, DRY WEIGHT, AND CARBON: A CORRECTION

The objective of this note is to point out the fact that the first nine equations published by Wiebe et al. (1975, table 2) were those appropriate for the Y on X regressions; they were not the functional regression equations as originally claimed. This mistake was discovered as a result of correspondence with F. A. Ascioti (Dip. di Biologia Animale Ed Ecologia Marina; Universita di Messina; Via Dei Verdi 75; 98100 Messina ITALY). This table 2 should have had the following equations in it:

Equation	*Regression equation*	*N*
1	$LOG(DV) = -1.434 + 0.820\ LOG(C)$	87
2	$LOG(WW) = -1.537 + 0.852\ LOG(C)$	70
3	$LOG(DW) = 0.499 + 0.991\ LOG(C)$	195
4	$LOG(DV) = -1.842 + 0.865\ LOG(DW)$	163
5	$LOG(WW) = -2.002 + 0.950\ LOG(DW)$	95
6	$LOG(DV) = 0.139 + 1.003\ LOG(WW)$	77
7	$LOG(BWW) = -1.947 + 1.050\ LOG(BDW)$	421
8	$LOG(BDV) = -1.887 + 1.007\ LOG(BDW)$	404
9	$LOG(BDV) = 0.005 + 0.981\ LOG(BWW)$	403

10	LOG(PDW	=	0.853 + 1.024	LOG(PC)	45
11	LOG(DV)	=	1.037 + 0.839	LOG(DW)	111
12	LOG(WW)	=	0.975 + 0.946	LOG(DW)	94
13	LOG(DV)	=	0.107 + 1.082	LOG(WW)	76

To prepare these GM functional regression equations (Ricker 1973:412), the original data were checked and log transformed, and the regressions recomputed. The variances and correlation coefficients remain essentially unchanged. Note that in Wiebe et al. (1975) and above, equations 1–10 are based on biomass standardized to per cubic meter while the remainder are not. Equations 6 and 10 in table 2 of Wiebe et al. (1975) also contained errors; the intercept of equation 6 was incorrectly printed as 0.670 rather than 0.067; the intercept of equation 10, which was 0.558, has been corrected to 0.853.

The equations listed above, when compared with those originally presented, provide estimates of x given y or y given x, which generally differ by less than 6% in the central part of the data set and by less than 15% in the tails of the data set. Samples similar in biomass and taxonomic composition to those used in this study, which we have analyzed for size of individuals as a function of taxonomic unit (Davis and Wiebe 1985), contain animals which typically range in size from 0.35 mm to 100 mm.

For a number of samples for which we reported carbon values, nitrogen values were also obtained from the CHN analyzers we used (Table 1, this note). Although carbon to nitrogen conversion factors exist in the literature, few are based on data ranging over as many hydrographic regimes as does data presented in Wiebe et al. (1975). Since a growing number of mathematical models use nitrogen rather than carbon as the basic currency, we take this opportunity to present these data (Fig. 1) and the resulting carbon/nitrogen ratio.

Functional regression of carbon versus nitrogen yielded the following significant ($P < 0.01$; $r^2 = 0.99$) relationship:

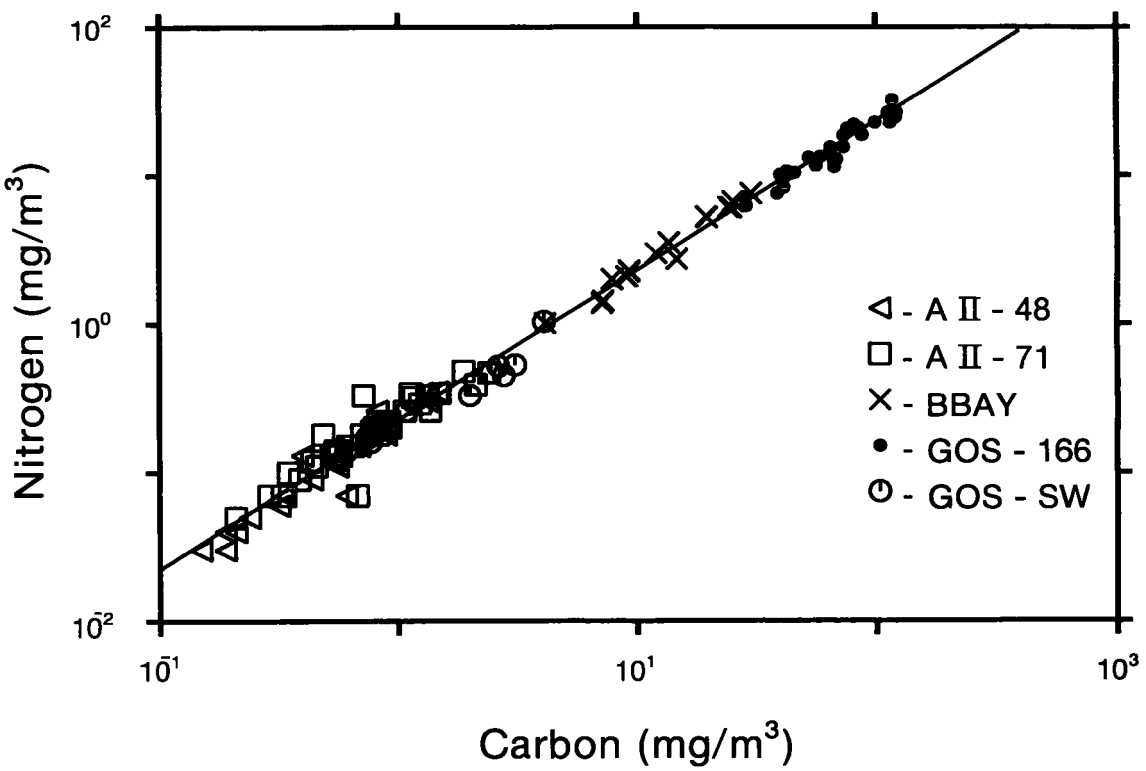

FIGURE 1.—Plot of data used in calculating the regression relating carbon and nitrogen in zooplankton collections from areas specified in Table 1.

TABLE 1.—Number of zooplankton samples for each cruise from which both carbon and nitrogen were measured. The general location of the stations for these samples are given in Wiebe et al. (1975).

Cruise or area	Date	No. of measurements	Diameter of net (mesh size)
Buzzards Bay	Jan.–June 1972	16	70 cm (240 μm)
Slope Water (RV *Gosnold*)	June–Aug. 1972	12	100 cm (333 μm)
Atlantis II 48 (Gulf of Mexico)	Nov. 1968	19	70 cm (240 μm)
Gosnold 166 (New York Bight)	June 1970	33	70 cm (240 μm)
Atlantis II 71 (Sargasso Sea)	Sept. 1972	39	100 cm (333 μm)

$$\text{Nitrogen (mg/m}^3) = -0.0247 + 0.2324 \text{ carbon (mg/m}^3)$$

Essentially the carbon/nitrogen ratio of the bulk zooplankton we collected is a constant (4.30) over a broad range of values and oceanographic habitats. As an atomic ratio, 5.02, this value is lower than that predicted by the Redfield ratio, 6.63 (Redfield et al. 1963), an indication that zooplankton are nitrogen rich relative to their phytoplankton counterparts.

Acknowledgments

We would like to express our appreciation to F. A. Ascioti for his correspondence and attention to detail which enabled us to correct the mistakes in our previous publication. This research was supported by NSF Grant OCE-8709962 and is Contribution No. 6839 from the Woods Hole Oceanographic Institution.

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ELECTROPHORETIC IDENTIFICATION OF EARLY JUVENILE YELLOWFIN TUNA, *THUNNUS ALBACARES*

Early juveniles, 13 mm standard length (SL) or larger, of yellowfin tuna, *Thunnus albacares*, and bigeye tuna, *T. obesus*, cannot be distinguished on the basis of meristic, morphological, or pigmentation characters (Matsumoto et al. 1972). Collette et al. (1984) reported that most species of the genus *Thunnus* can be distinguished at the larval stage by melanophore patterns. Matsumoto et al. (1972) and Nishikawa and Rimmer (1987) suggested that *T. albacares* and *T. obesus* larvae can be separated by the respective absence or presence of postanal ventral melanophores. Confirmation of the identification of *T. albacares* larvae has been obtained through laboratory rearing studies (Harada et al. 1971; Mori et al. 1971). However, the use of postanal ventral pigmentation patterns as reliable characters to distinguish yellowfin and bigeye tuna larvae has been questioned by Richards and Pothoff (1974). Nishikawa and Rimmer (1987) stated that it is virtually impossible to identify to species the early juvenile stages, 15 to 60 mm SL, of *Thunnus* because larval pigmentation patterns become obscured and are no longer diagnostic. Furthermore, Pothoff (1974) was unable to separate *T. albacares* and *T. obesus* as early juveniles, 8 to 100 mm SL, on the basis of osteological characters.

Electrophoresis of water soluble proteins has been used to distinguish morphologically similar larval and early juvenile marine fishes (Morgan 1975; Smith and Crossland 1977; Sidell et al. 1978; Smith and Benson 1980). Sharp and Pirages (1978) presented starch gel electrophoretic patterns for several loci of adults of many scombrid species, including most members of the genus *Thunnus*. Although electrophoretically very similar, adults of yellowfin and bigeye tuna can be unambiguously distinguished by the electrophoretic pattern of the muscle isozyme of glycerol-3-phosphate dehydrog-

enase (alpha glycerol phosphate). This locus has been used to identify adults of the genus *Thunnus* in the absence of complete morphological data (Dotson and Graves 1984). This paper describes an application of the above techniques, modified for work with small tissue samples, to the identification of an opportunistic collection of early juvenile tuna, in excellent morphological condition, which were frozen shortly after capture. The early juveniles in this collection encompassed the pigmentation patterns reported for both *T. albacares* and *T. obesus*.

Specimens were collected aboard the MV *Royal Polaris*, a San Diego-based sportfishing boat, about 1 km off Clipperton Island in the eastern Pacific (lat. 10°23'N, long. 109°15'W), 8 May 1986, from hours of 2100 to 2400. The early juveniles were caught underneath floodlights at a depth of about 1 m with a fine (1 mm) mesh, long-handled dip net. They were not present at the surface. After each pass, the dip net contents were sorted for scombrid larvae. Approximately 100 specimens were collected, most of which were quickly frozen in seawater.

Adult specimens of *T. albacares* and *T. obesus* were collected by hook and line off the Pacific coast of southern and northern Baja California, Mexico, respectively. White muscle tissue samples were removed from freshly caught specimens and quickly frozen.

The early juveniles collected off Clipperton Island were thawed in the laboratory and examined under a dissecting microscope. Those juveniles positively identified to the morphologically indistinguishable *T. albacares/T. obesus* complex were measured for total length (TL) to the nearest millimeter and examined for postanal ventral pigmentation pattern. Heads were removed and placed in 95% ethanol for otolith studies. The remaining trunk and tail musculature was placed in a small (1.0 mL) microfuge tube, and 60 μL of cold grinding buffer (0.1 M Tris, pH 7.5) was quickly added. Tissues were homogenized with a cold ground-glass rod contoured to fit snugly within the microfuge tube. Approximately 10 seconds of rod rotation were required to completely disrupt the tissues. The homogenate was centrifuged for 2 minutes in a microfuge and stored on ice until electrophoresis.

Two grams of adult tissue were disrupted for approximately 20 seconds in 4 volumes of cold grinding buffer in a motor-driven, ground-glass tissue homogenizer. The homogenate was centrifuged at 5,000 *g*, 4°C, for 10 minutes. The supernatant was removed, diluted 10:1 with cold grinding buffer, and stored on ice until electrophoresis.

Horizontal starch gel electrophoresis was performed on 12% (W/V) gels run in the Tris/Citrate II system of Selander et al. (1971). Gels were run at 45 to 50 mA for 3.5 hours. Glycerol-3-phosphate dehydrogenase was stained using the protocol of Shaw and Prasad (1970). Three sets of standards composed of the supernatants of muscle tissue homogenates of adult yellowfin and bigeye tuna were placed in each gel to score the early juveniles.

A total of 77 early juveniles, ranging in length from 10 to 21 mm TL, were processed. Glycerol-3-phosphate dehydrogenase activity was scored for 68 individuals. All early juveniles displayed a muscle-type glycerol-3-phosphate dehydrogenase band of low anodal mobility, identical to that of the yellowfin tuna adults (Fig. 1). No individuals with the faster migrating *T. obesus* glycerol-3-phosphate dehydrogenase band were detected.

The lack of bigeye tuna juveniles in this study could be the result of two possibilities: either the early juveniles were all yellowfin tuna or both yellowfin and bigeye tuna early juveniles share a muscle-type glycerol-3-phosphate dehydrogenase isozyme of similar electrophoretic mobility. However, differential ontogenetic expression of electrophoretically distinct isozymes has not been reported for fishes in studies that have used adult allozymes to identify larvae or early juveniles (Morgan 1975; Smith and Crossland 1977; Sidell et al. 1978; Smith and Benson 1980) or in investigations of ontogenetic expression of electrophoretic loci (Shaklee et al. 1974; Siebenaller 1984). Thus, the electrophoretic similarity of the glyceraldehyde-3-phosphate alleles of the early juveniles investigated in this study most likely indicates that they were all yellowfin tuna.

On the same trip during which the early juveniles were collected at Clipperton Island, about 300 adult yellowfin tuna were caught on hook and line but no bigeye tuna were taken. Histological examination of ovarian tissue from several of the adult yellowfin tuna revealed postovulatory follicles, indicating that spawning was taking place (Anonymous 1987). On the basis of this information, it is not unexpected that all the early juveniles identified electrophoretically in this study proved to be *T. albacares*.

A wide range of postanal ventral pigmentation patterns (red and black) was displayed by the early juveniles. Since these specimens were collected at night, the pigment cells, when present, were distinct and brightly colored as reported by Matsumoto et al. (1972). While some individuals had no melanophores in this region, others had from one to eight.

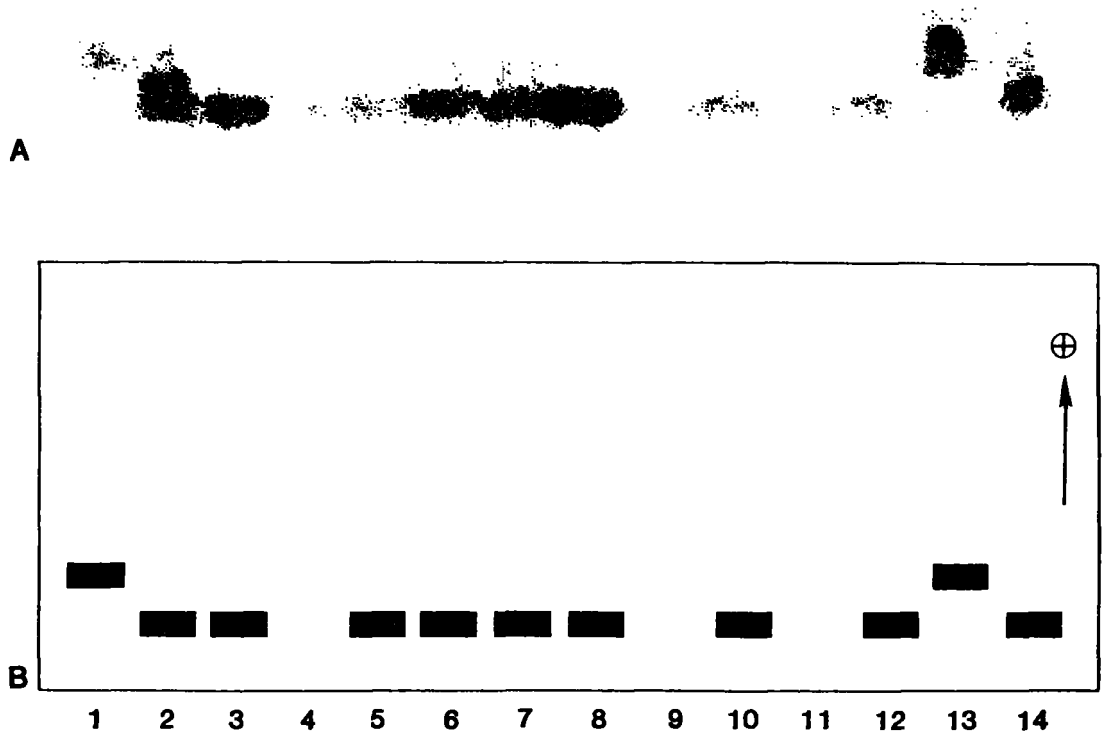

FIGURE 1.—Photograph (A) and line drawing (B) of a gel demonstrating electrophoretic mobilities of muscle-type glycerol-3-phosphate dehydrogenase alleles of yellowfin and bigeye tuna. Bigeye tuna display an allele with a greater anodal mobility. The gel includes adult bigeye (lanes 1 and 13) and yellowfin (lanes 2 and 14) tuna standards and 7 early juveniles, all identified as yellowfin tuna. Note that three individuals (lanes 4, 9, and 11) did not have sufficient activity to stain.

According to Matsumoto et al. (1972) and Nishikawa and Rimmer (1987), yellowfin larvae less than about 12 mm SL have no black pigment spots in the ventral tail region. However, Mori et al. (1971) reported and illustrated that there is black pigmentation on the ventral edges of the tail in laboratory-reared yellowfin larvae at 7.8 mm TL. Twenty-one individuals in the 10 to 12 mm TL size range were electrophoretically typed as yellowfin tuna in this study. Six of these early juveniles had black postanal ventral pigmentation (characteristic of bigeye tuna), while 15 had no black postanal ventral pigmentation (characteristic of yellowfin tuna).

Variability in larval and early juvenile pigmentation within species, including large changes in pigmentation over small size ranges, is found within many marine fishes (Powles and Markle 1984). Richards and Pothoff (1974) have suggested that the variability of postanal ventral pigmentation is not consistent with specific differentiation within the *T. albacares*/*T. obesus* complex. This study supports their claim.

Early life history studies are necessary for an understanding of recruitment within each species of tuna. Due to the morphological similarity of yellowfin and bigeye tuna larvae and early juveniles, specific separation has not been possible. This study provides a simple method for identifying yellowfin and bigeye tuna larvae and early juveniles. With this technique and additional material, it may be possible to find a morphological character that will allow rapid identification of these two species.

Acknowledgments

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A COMPARISON OF DEMERSAL ZOOPLANKTON COLLECTED AT ALLIGATOR REEF, FLORIDA, USING EMERGENCE AND REENTRY TRAPS

Demersal zooplankton have been shown to be important components of a number of marine communities, including coral reefs (Porter and Porter 1977; Alldredge and King 1977), kelp beds (Hammer 1981), and other habitats (Thomas and Jelley 1972). They probably play an important role in the flux of particulate material through benthic communities (Porter and Porter 1977). Demersal zooplankton can also be important prey for fish and other consumers (Alldredge and King 1977, 1980).

Demersal zooplankton are usually sampled by techniques that take advantage of their migration into or out of the plankton. Studies by Alldredge and King (1980, 1985) and Youngbluth (1982) suggest

that sampling methods used to collect demersal zooplankton can have a significant effect on the numbers and kinds of animals collected. The most widely used method to date is emergence trapping, in which zooplankton are collected as they migrate out of the substrate, e.g., Porter and Porter (1977). Another method, reentry trapping, captures zooplankton as they enter the substrate, e.g., Alldredge and King (1980). A primary purpose of this study was to compare results from simultaneous emergence and reentry trapping, and verify Alldredge and King's (1980) finding that reentry traps capture significantly more zooplankton than emergence traps.

Horizontal currents are likely to have major but variable effects on the transport of demersal organisms in the plankton. Organisms migrating high into the water column are likely to be transported laterally to a greater extent than those that remain in the near-bottom layer, as Alldredge and King (1985) have suggested. Thus, the implicit assumption of some other investigators that demersal zooplankton are characteristic residents of a habitat needs qualification. Horizontal transport of migrating demersal zooplankton is probably an important recruitment mechanism and a means by which planktivorous fish associated with reefs and other structures are supported. Demersal zooplankton have been shown to be associated with sand bottoms by Alldredge and King (1977, 1980), so sand bottoms might be an important source of demersal zooplankton for reef communities. Therefore, our purpose in this study was also to assess the abundance of demersal zooplankton on sand bottom habitat. The study addressed the questions: how abundant are different taxa of demersal zooplankton associated with sand bottom habitat? Can different trapping techniques distinguish zooplankters with different propensities for horizontal transport by currents? How do the abundance and taxonomic composition of demersal zooplankton on open carbonate sand compare with the finding of others studying similar sand bottoms?

Materials and Methods

Study sites were located approximately 1.8 km east of Alligator Reef Buoy, ca. 7.5 km southeast of Upper Matecumbe Key in the Florida Keys (lat. 24°41.26'N, long. 80°35.68'W). The sites were characterized by a subtidal, carbonate sand bottom that sloped gently from depths of 2–4 m to depths of over 40 m. Macrophytes occurred sparsely on the bottom (principally *Thalassia* sp.), with the closest coral structure and associated fish populations several hundred meters downstream. Currents were minimal (<0.05 m s^{-1}) and flowed to the northeast, parallel to the axis of the Gulf Stream just offshore.

Sampling at the site was conducted with the aid of scuba, supported by the NOAA-National Undersea Research Program's RV *Seahawk*, which operated in the Florida Keys region during March 1985.

Demersal zooplankton were sampled simultaneously by emergence trapping and reentry trapping. The emergence traps were a simplified version of those used by Hobson and Chess (1979), consisting of a single cone of 95 μm mesh netting 1 m high and 21 cm diameter at the mouth (Fig. 1). The mouth of the net was weighted with lead weights sewn into the mouth collar to aid placement on the bottom. A 1 L polyethylene bottle with a polyethylene funnel in the throat was attached to the upper end of the net; the bottles' natural buoyancy extended the traps. Reentry traps were square polyethylene pans, 21 cm per side and 5 cm deep, with removable snap-top lids, approximately one-third filled with defaunated local sand.

Divers deployed six of each type of trap in adjacent groups just after dusk and retrieved them just after dawn on two successive nights in March 1985. Reentry traps were closed and trap bottles from emergence traps capped by divers before return to the surface. The moon was nearly new and rose late each night, thus providing little illumination. The first night's collections were made for 12.75 hours at a depth of 7 m and the second night's for 11.5 hours at a depth of 20 m.

Animals in the collection bottles of the emergence traps were concentrated on a 95 μm mesh sieve, washed into sample bottles, and fixed in a buffered formalin-Rose Bengal solution (ca. 5% formalin final strength). Animals that had entered the reentry traps were washed from the sand with fresh water, causing them to release their grasp on sand grains (R. Higgins[1]). The contents of each trap were washed at least 5 times, and until no further animals could be seen in the wash water. All washings were sieved through a 95 μm mesh sieve. The retained material was then poured into sample bottles and fixed as above.

The stained, fixed animals in each sample were examined, identified, and counted with a stereomicroscope. Identifications were made to genus and

[1]R. Higgins, Smithsonian Institution, Washington, DC 20560.

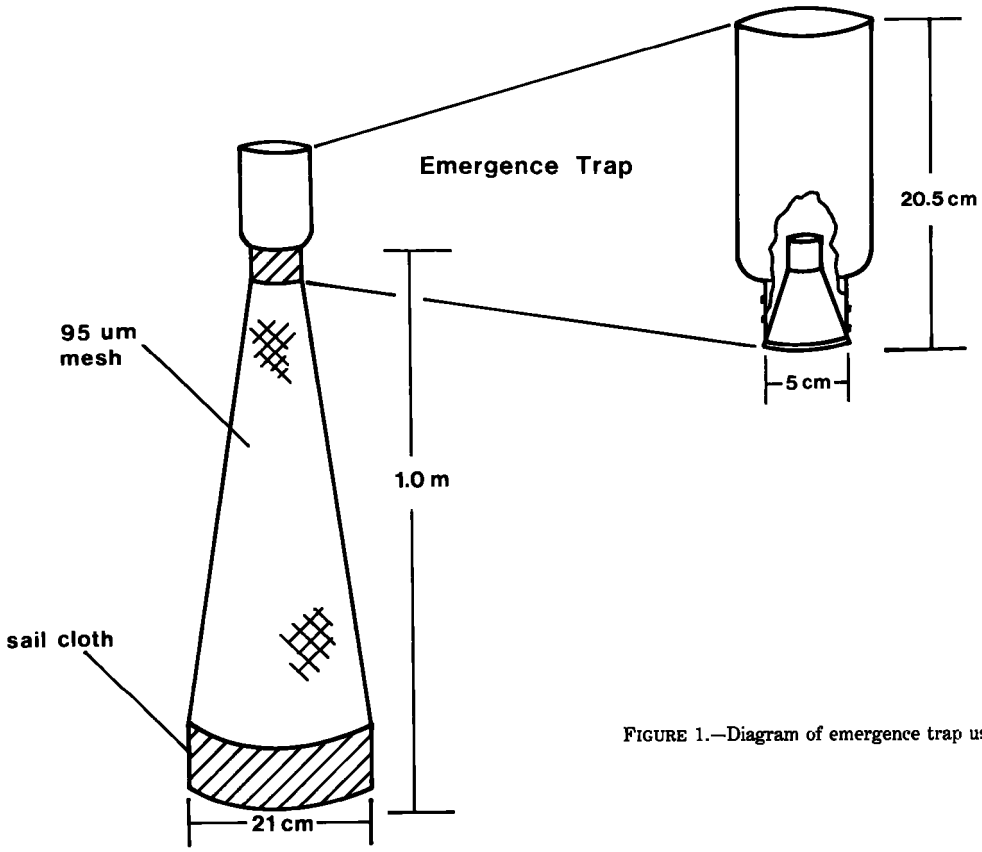

FIGURE 1.—Diagram of emergence trap used in this study.

species when possible; numbers of major taxa and groups are presented here for simplicity and comparative purposes.

Results

The zooplankton caught in the traps at Alligator Reef were dominated by copepods. Other taxa and categories that were collected included chaetognaths, nematodes, ostracods, polychaetes, cumaceans, isopods, amphipods, and mysids, as well as numerous others that were less common or frequently caught (Table 1). Many of these groups, such as the harpacticoid copepods, are well known as benthic or near-bottom forms. Others, such as the calanoid copepods, are known as primarily planktonic animals that are sometimes observed close to the bottom or other substrate. Many larval forms of benthic macroinvertebrates were captured, especially settling stages, such as barnacle cyprids and megalopae.

Comparisons of the total mean numbers of animals caught by each trap type and at each location show that approximately 4 times as many animals were caught by reentry traps as by emergence traps and that about twice as many animals were captured at the 7 m site as at the 20 m site (Table 1). Twelve common groups together accounted for 97.9% of all the animals caught. The results of two-way ANOVAs showed that reentry traps captured significantly more harpacticoid and cyclopoid copepods, ostracods, mysids, polychaetes, and nematodes than emergence traps, while the emergence traps captured significantly more calanoid copepods and isopods (Table 2). Significantly more cumaceans, gammarid amphipods, polychaetes, and nematodes were captured at the 20 m site than at the 7 m site, while significantly more calanoid copepods and chaetognaths were captured at the shallower location (Table 2). The two-way ANOVAs showed significant interaction effects between the trap types and sampling locations on the numbers of harpacticoid and

TABLE 1.—Demersal zooplankton captured in reentry and emergence traps at sand bottom sites (7 m and 20 m) near Alligator Reef, Florida in March 1985. Data are mean numbers of animals m^{-2} (SE).

	Emergence		Reentry	
Group	7 m	20 m	7 m	20 m
Harpacticoids[1]	754 (188)	3,040 (726)	16,108 (2,289)	8,866 (845)
Cyclopoids[1]	2,039 (508)	740 (165)	5,943 (1,071)	3,713 (478)
Nematodes[1]	11 (11)	13 (9)	8,840 (1,241)	823 (121)
Calanoids[1]	2,023 (421)	359 (128)	231 (80)	574 (209)
Copepod nauplii[1]	830 (248)	338 (99)	130 (53)	515 (121)
Ostracods[1]	51 (14)	35 (15)	498 (93)	360 (80)
Chaetognaths[1]	289 (47)	17 (8)	357 (70)	126 (65)
Halacarids	4 (4)	0	538 (160	0
Polychaetes[1]	29 (27)	69 (42)	94 (39)	314 (56)
Caprellid amphipods	0	117 (38)	4 (4)	170 (18)
Gammarid amphipods[1]	11 (5)	100 (49)	54 (19)	119 (32)
Cumaceans[1]	14 (5)	74 (51)	58 (23)	101 (18)
Mysids[1]	7 (5)	39 (8)	72 (27)	43 (18)
Larvaceans	112 (87)	0	29 (29)	11 (11)
Isopods[1]	62 (15)	35 (11)	7 (7)	33 (9)
Lancelets	0	0	14 (7)	69 (9)
Pycnogonids	4 (4)	39 (34)	0	0
Tanaids	0	36 (11)	0	0
Cyphonautes	0	0	0	29 (13)
Penaeids	0	9 (5)	0	18 (7)
Chiton larvae	0	0	11 (7)	7 (5)
Pagurid crabs	0	4 (4)	7 (5)	4 (4)
Cyprids	0	0	11 (7)	0
Hippid crabs	0	0	0	7 (5)
Magelona polychaetes	0	4 (4)	0	0
Fish larvae	0	4 (4)	0	0
Brachyuran crabs	0	4 (4)	0	0
Totals	6,240	5,076	33,006	15,902
Trap totals	11,316		48,908	
Site totals: 7 m: 39,250 20 m: 20,978				
Grand total 60,228				

[1]"common" groups caught by both traps at both sites.

TABLE 2.—Results of 2-way ANOVAs comparing effects of sampling location and trap type on numbers of animals caught from 12 common groups. Data are mean/m^2 and F value for associated comparisons for each category; significantly higher means are underlined. For all comparisons df = 1, 19.

	Location			Trap			Interaction
Group	7 m	20 m	F	Emergence	Reentry	F	F
Harpacticoids	8,431	6,218	2.81	1,793	12,487	65.57**	14.33**
Cyclopoids	3,991	2,361	4.14	1,449	4,828	17.83**	1.17
Nematodes	4,426	454	36.80**	12	4,842	54.20**	41.70**
Calanoids	1,127	476	6.45**	1,267	402	11.39**	14.53**
Copepod nauplii	480	427	3.12	606	305	3.33	4.00
Ostracods	274	207	1.00	43	424	36.30**	1.75
Chaetognaths	323	77	19.51**	165	242	1.88	1.00
Polychaetes	61	203	12.07**	47	204	14.82**	3.69
Gammarid amphipods	32	110	7.26*	51	87	1.00	1.00
Cumaceans	36	89	4.41*	41	79	2.32	2.97
Mysids	40	41	1.00	22	58	4.92*	3.45
Isopods	34	33	1.00	49	20	6.94*	5.41*

* = $P < 0.05$, ** = $P < 0.01$.

calanoid copepods, isopods, and nematodes caught (Table 2), indicating that the capture rates of the two trap types varied between locations. Differences in the types and numbers of animals caught by each trap are more important, however.

Reentry traps were much more effective than emergence traps at capturing a greater variety of animals. The most striking differences are the much larger numbers of harpacticoid and cyclopoid copepods captured in reentry traps. In addition to quantitative differences the reentry traps also caught individuals of six groups that were not found in the emergence traps (Table 1). The six groups included the lancelets and five types of demersal larvae.

Conversely, emergence traps were more effective at capturing calanoid copepods and isopods. Specimens of five other taxa were captured only in emergence traps (Table 1).

Analysis of the capture rate of each common group by the two trap types shows significantly different assemblages (χ^2 = 881068, df = 11, $P << 0.001$) (Fig. 2a). Furthermore, each trap type caught some relatively rare groups, meaning that the lower capture rate of the emergence traps did not prevent them from capturing groups that did not appear in the reentry traps. Analysis of the capture frequencies of these rarer groups shows that the two trap types capture different assemblages of organisms (χ^2 = 25806, df = 9, $P << 0.001$) (Fig. 2b). Therefore, the reentry and emergence traps sampled different fauna or sampled the same fauna differently.

Discussion

Varying migration patterns and swimming behaviors by the various taxa and groups can explain the differences between the assemblages caught by the two trap types. Ascending animals would have to move 1 m off the bottom in order to be captured by the emergence traps. Descending animals would not have been captured at all by the emergence traps, but would only have needed to be a few cm off the bottom to enter the reentry traps. Thus, reentry traps are more likely to capture demersal organisms during their migration than emergence traps if many of these organisms never move very far up into the water column, as Alldredge and King (1985) have shown. Reentry traps also captured settling larvae, which presumably are migrating in only one direction prior to establishing a sessile mode of life. Such larval forms were a small fraction of the total numbers of animals caught, but could be a significant portion of the reentering fauna at times. Both trap types may have also captured some animals that are holoplanktonic as noted by Robichaux et al. (1981), despite our efforts to prevent this during deployment and recovery of the traps. Some animals may have entered the traps by crawling rather than from the plankton, as Scheibel (1974) observed. Finally, placement of the traps after dusk may have missed animals migrating at or before dusk, but the errors caused by this artifact, as well as errors due to incomplete recovery of animals, are not likely to alter our results significantly.

Another possible explanation for at least some of the differences between capture rates of the two trap types is differential avoidance of one trap type, in this case the emergence traps. Given that emergence traps consist of materials quite unlike those that demersal zooplankton would normally encounter it should not be surprising that they might seek to avoid contact with them. The narrow funnel placed in the mouth of the collection bottles, while necessary to retain animals that have entered the bottle, may exclude others altogether. Some demersal zooplankton, such as calanoid copepods, are well known to exhibit an escape response when placed in contact with surfaces. Reentry traps, on the other hand, work partly by replicating natural sand substrate, reducing the potential for avoidance.

The results show clearly that different sampling techniques yield variable numbers of animals, even within the same taxon, and collect different groups of animals. Thus, evaluation of the demersal zooplankton depends strongly on sampling techniques. Adoption of a single standard sampling technique might appear to be a resolution of the problem, but a standard approach should sample all the organisms that exhibit demersal behavior in a given area, and neither emergence trapping nor reentry traping does. Furthermore, Stretch (1985) has observed that not all members of a demersal population migrate each night, so trapping techniques that depend on animal migration must consistently underestimate the actual abundance of demersal organisms in association with a given substrate. Tendency to migrate may vary among species, within the life cycle of a given species and from day to day, making accurate sampling of the demersal zooplankton by trapping a logistical impossibility. Collection techniques that directly sample demersal organisms in or on the substrate, such as airlift sampling (Stretch 1985) or sediment coring techniques commonly used to sample meiofauna, should give more accurate abundance estimates, but must be used in conjunction with one or more trapping

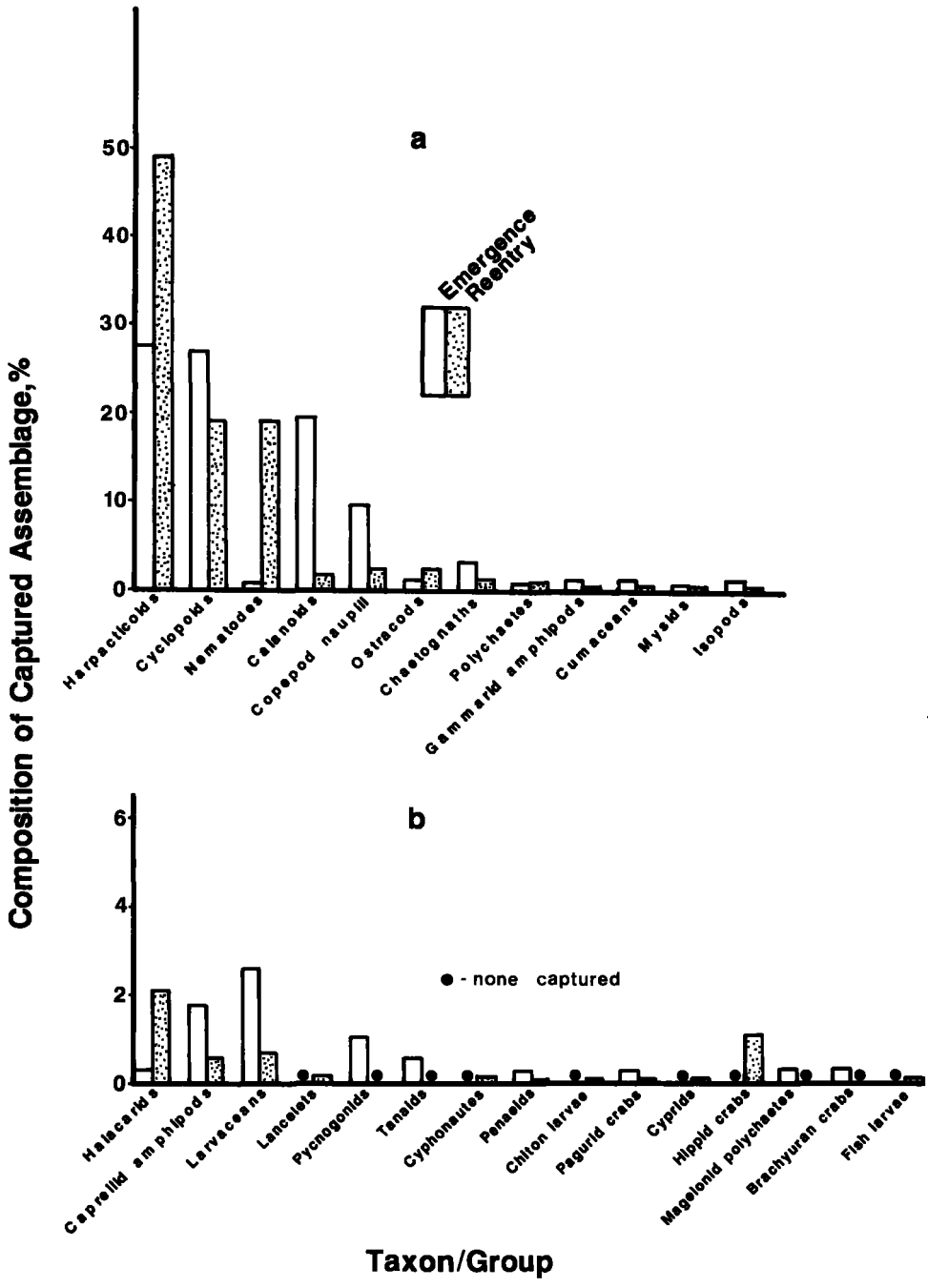

FIGURE 2.—Percentage of the total animals caught by each trap type by taxon or group, in rank order of total abundance, pooled over sites; a) common groups, b) rare groups.

techniques to distinguish migratory from nonmigratory populations.

Comparisons of demersal zooplankton abundances among studies are also made difficult by variation among the trap types and approaches used. Alldredge and King (1980) compared reentry and emergence traps, showing as we have that reentry traps captured very much larger numbers and different proportions of demersal organisms. Aside from studies by Stretch (1985) and ourselves (unpubl. data), we are unaware of any effort to use a direct sampling technique to calibrate a trapping technique. Thus, published abundance estimates for demersal zooplankton abundance are probably low and biased, reflecting the preponderant use of emergence trapping.

Robichaux et al. (1981) pointed out that animals entering traps by crawling can be a significant artifact. Such contamination would probably be a greater problem for reentry traps than for emergence traps. Our reentry traps captured large numbers of nematodes and harpacticoid copepods, which can enter by crawling, but even when they are eliminated altogether from the trap totals, reentry traps still caught twice as many animals as emergence traps (Table 1). Furthermore, at least some nematodes and harpacticoids do swim freely, even if they do not move very far up into the water column, as Alldredge and King (1985) have shown. Thus, we think that reentry trapping reliably yields higher estimates of demersal zooplankton abundance that are more realistic than results from emergence trapping but probably not truly accurate.

Robichaux et al. (1981) also argued that contamination of demersal zooplankton traps by holoplanktonic and crawling organisms causes an overestimate of the actual importance of demersal zooplankton in benthic food webs. We dispute this view on several grounds. First, the emergence trapping technique used by Robichaux et al. (1981), as is the case with others' use of emergence trapping, probably yielded significant underestimates of the actual abundance of demersal zooplankton, as we discuss above. Second, we suspect that all trapping techniques are likely to miss animals that are not migrating actively or that avoid traps, causing further population underestimates. Finally, estimates of demersal zooplankton populations resident within a given habitat may fail to reflect the actual availability of these animals as consumers or prey via transport.

Sand bottom habitats may be important sources of demersal zooplankton for consumers in other habitats. Currents can carry demersal organisms passively to other habitats. Animals that migrate high into the water column, such as the groups captured especially well by emergence traps, may be carried relatively great distances compared with those that crawl or stay within the near-bottom boundary layer. Furthermore, off-reef foraging by reef dwellers may allow exploitation of demersal organisms on sandy bottoms in the absence of advection. If so, estimates of demersal zooplankton abundance derived from reentry trapping will again be realistic, if not accurate, from the standpoint of community ecology. Therefore, demersal zooplankton are potentially quite important to marine benthic communities, even if the techniques used to sample them are imperfect.

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NOAA Technical Reports NMFS published during first 6 months of 1988.

63. Stock assessment of the Atlantic menhaden, *Brevortia tyrannus* fishery. By Douglas S. Vaughan and Joseph W. Smith. January 1988, iii + 18 p., 13 tables, 17 figs.
64. Illustrated key to penaeoid shrimps of commerce in the Americas. By Isabel Pérez Farfante. April 1988, iv + 32 p., 49 figs.
65. History of whaling in and near North Carolina. By Randall R. Reeves and Edward Michell. March 1988, iii + 28 p., 5 tables, 10 figs.
66. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. By M. James Allen and Gary B. Smith. April 1988, iii + 151 p., 8 tables, 4 figs.

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ERRATA

Fishery Bulletin Vol. 86, No. 3

Hoss, Donald E., Linda Coston-Clements, David S. Peters, and Patricia A. Tester, "Metabolic responses of spot, *Leiostomus xanthurus*, and Atlantic croaker, *Micropogonias undulatus*, larvae to cold temperatures encountered following recruitment to estuaries," pages 483–488.

Bottom of page 484 should read as follows:

FIGURE 1.—Representative water-temperatures, salinities, and developmental stages of larval spot from the spawning area to Beaufort Inlet, North Carolina. Drawings from Powell and Gordy (1980) and Lippson and Moran (1974).

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