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Notes

Seattle, Washington

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Fishery Bulletin

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DISTRIBUTION, ABUNDANCE, AND AGE AND GROWTH OF THE TOMTATE, *HAEMULON AUROLINEATUM*, ALONG THE SOUTHEASTERN UNITED STATES COAST[1]

CHARLES S. MANOOCH III[2] AND CHARLES A. BARANS[3]

ABSTRACT

Tomtates, *Haemulon aurolineatum*, were widely distributed over sponge-coral habitats throughout the South Atlantic Bight region in depths of 9 to 55 m, although they were occasionally caught in large numbers over sandy bottom habitats. Fish were most common in offshore areas during winter and were not taken in waters of <10°C south of Cape Fear, N.C. Juveniles (≤148 mm TL) were caught in the same geographical areas as adults, but were collected in warmer waters than adults during fall and winter. Spawning occurred during the spring.

Individuals collected by hook and line and trawl were aged by scales and otoliths. Back-calculated mean total lengths were from 103.0 mm at age I, to 280.5 at age IX. The von Bertalanffy growth equation is $l_t = 310\,(1 - \exp - 0.22017\,(t + 1.28))$, where t is age in years, and l_t is total length at age. The oldest fish sampled was age IX, 289 mm TL. Annual total mortality based on catch curves from 1,496 fish landed by the recreational fishery from 1972 to 1978 was 59% (instantaneous total annual mortality = 0.89). We found that the tomtate grows faster, does not live as long, and has a higher natural mortality rate than most other reef fishes previously studied in the South Atlantic Bight.

The tomtate, *Haemulon aurolineatum*, is a small grunt (Haemulidae), which occurs from Cape Cod, Mass., to Brazil, including the Caribbean, Gulf of Mexico, and Central American coast. The species, previously referred to as *Bathystoma rimator*, *B. aurolineatum*, and *Haemulon rimator* (Courtenay 1961), is known vernacularly as xira in Brazil; cuji in Venezuela; rancho, juez, and chankay in Mexico; and mulita, mula, mariquita, and maruca in Puerto Rico.

The tomtate is taken primarily by hook and line off the southeastern United States and by traps, hook and line, and trawl in the more southern areas of its range. Unfortunately, commercial landings of tomtates in the United States are reported in the collective term "grunts," which includes many different species of the family and therefore precludes species identifications that are needed for fishery management. A Soviet-Cuban cooperative fisheries research program on the Campeche Banks revealed the tomtate as the main demersal species caught by trawl from 1962 to 1972 (Sokolova 1969; Sauskan and Olaechea 1974). Also, exploratory trawling off South Carolina found large quantities of tomtates (Wenner et al. 1979a).

Recreational headboat[4] fishermen fishing from North Carolina to Cape Canaveral, Fla., caught an average of 23.2 t (metric tons) of tomtates in 1976 and 1977 (Dixon[5]). This species was the most commonly caught haemuline, although second in weight landed to the white grunt, *Haemulon plumieri*.

In this paper we describe the relative abundance, spatial and temporal distributions, spawning, age, growth, and mortality for tomtates along the southeastern United States.

METHODS

Distribution and Relative Abundance

Eight groundfish survey cruises spanning all four seasons (Table 1) were conducted on the con-

[1]Contribution No. 192, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA; No. 189, MARMAP Program; No. 127, South Carolina Marine Resources Center, Marine Resources Institute.

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[4]A boat for hire where anglers are charged on a per person basis.

[5]R. L. Dixon, Southeast Fisheries Center Beaufort Laboratory, NMFS, NOAA, Beaufort, NC 28516, pers. commun. January 1978.

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TABLE 1.—Groundfish cruises of the RV *Dolphin*.

Cruise	Dates	No. of trawls	No. of tows with tomtates	No. of tomtates
DP-7305	23 Oct -16 Nov. 1973	86	18	2,075
DP-7402	1 Apr. - 9 May 1974	112	19	442
DP-7403	13 Aug.-19 Sept. 1974	87	14	581
DP-7501	16 Jan. -10 Apr. 1975	92	10	1,212
DP-7503	30 Aug.-19 Sept. 1975	87	20	1,298
DP-7601	12 Jan. - 7 Feb. 1976	86	15	4,005
DP-7603	28 Aug.-21 Sept. 1976	89	15	1,749
DP-7701	17 Jan. - 9 Mar. 1977	93	11	3,260

tinental shelf and upper continental slope between Cape Fear, N.C., and Cape Canaveral, Fla., except in spring 1974 when sampling extended to Cape Hatteras. A preassigned number of stations was selected randomly (Grosslein 1969) with a set number in each of six depth zones (9-18 m; 19-27 m; 28-55 m; 56-110 m; 111-183 m; 184-366 m). Bottom water temperatures were measured at each station with mechanical or expendable bathythermographs.

Thirty-minute trawls were made continuously (day and night) from the RV *Dolphin*, at 6.5 km/h with a towing wire scope of 2.5-3.0:1. The trawl was a 3/4-scale version of a "Yankee No. 36" with a 16.5 m footrope, 11.9 m headrope, and 1.3 cm stretch mesh cod end liner (Wilk and Silverman 1976).

Fork lengths (later converted to total lengths) of all fish collected by trawl were recorded to the nearest centimeter. Frozen fish samples were taken to the laboratory for further investigations.

An index of relative abundance (Musick and McEachran 1972) was calculated for each depth zone by the following expression:

$$\text{Index of Relative Abundance} = \frac{\Sigma \ln (x+1)}{n_h}$$

where n_h = number of trawls in the hth depth zone, and x = number of individuals for each tow in a given depth zone. Because previous investigators have shown that trawl catches are usually distributed as a negative binomial (Elliott 1971; Taylor 1953), a $\ln (x+1)$ transformation was made on the relative abundance data to permit statistical tests to determine if the differences among habitats within depth zones were significant.

Estimates of biomass standing stock were calculated with both transformed, $\ln (x+1)$, and untransformed data for comparison of the resulting values. The stratified mean catch/tow (Cochran 1977) was calculated by the expression:

$$\bar{y}_{st} = \frac{1}{N} \sum_{h=1}^{k} [N_h \bar{y}_h]$$

where $\bar{y}_{st}$ = stratified mean catch(kg)/tow,
N = total area,
N_h = area of hth depth zone (from planimeter chart measurements),
$\bar{y}_h$ = mean catch/tow in the hth depth zone, and
k = number of zones in the set.

The area of live-bottom habitat in each depth zone (≈14.5%) was estimated from the frequency of occurrence of sponge and coral in catches during 5 yr of bottom trawling with the stratified random sampling design. The areas of sandy-bottom habitats were obtained by subtraction. The estimated population variance of the mean catch(kg)/tow was also calculated by Clark and Brown (1977):

$$S^2 = \frac{1}{N} \sum_{h=1}^{k} [N_h \bar{y}_h^{\,2}] - N\bar{y}_{st}^{\,2} + \sum_{h=1}^{k} S_h^{\,2} \left[(N_h - 1) + \frac{(N_h - N)}{N} \frac{(N_h - n_h)}{n_h} \right]$$

where S^2 = estimated population variance, and
$S_h^{\,2}$ = variance of the hth zone.

The mean catch/tow ($\bar{y}_h$) of the transformed $\ln (x+1)$ data was estimated for each depth zone following the methodology of Bliss (1967):

$$E(\bar{y}_h) = \exp (\bar{y}_h + S_h^{\,2}/2)$$

where $E(\bar{y}_h)$ = the estimated (retransformed) mean catch(kg)/tow in the hth depth zone, $\bar{y}_h$ and $S_h^{\,2}$, both expressed in logarithmic units, are the zone mean and its variance. The same methodology was applied to obtain the stratified mean catch/tow from transformed data for the whole study area. Biomass estimates were expanded by the area swept method (Rohr and Gutherz 1977), using

$$SS_{\text{tot}} = \sum_{h=1}^{k} (\bar{P}_h)\ (A_h)$$

where SS_{tot} = total standing stock,

$\bar{P}_h$ = average population expressed as kilograms per km^2 in the hth depth zone, and

A_h = total area of the hth depth zone.

The sweep of the "3/4 Yankee trawl" was 8.748 m (Azarovitz[6]), and 3.241 km was the distance covered during a standard trawl. It should be noted that all estimates were minimum estimates because the sampling efficiency of our gear with regard to tomtates was unknown. Standing stock values calculated for sandy-bottom areas incorporated such a large number of zero catches that the transformation did not normalize the data, so the resulting values should be considered suspect.

Age and Growth

Scales, otoliths, fish lengths, and fish weights were collected from 1,496 tomtates from the recreational headboat fishery operating from North Carolina to Cape Canaveral from 1972 through 1978 and from approximately 100 juvenile fish collected by research trawling off South Carolina. Total fish length was recorded in millimeters and weight in grams.

Scales were removed from beneath the tip of the posteriorly extended pectoral fin, soaked in a one-tenth aqueous solution of phenol, cleaned and mounted dry between two glass slides, and viewed at 40× magnification on a scale projector. Measurements were made and recorded from the scale focus to each annulus and to the scale edge in the anterior field for marginal increment analyses and back-calculating fish length at the time of annulus formation.

Otoliths (sagittae) were removed by making a transverse cut in the cranium with a hacksaw midway between the posterior edge of the orbit and the preopercle. The skull was pried open and the otoliths were removed with forceps, washed in water, and stored dry in labeled vials. Rings were counted by placing the otoliths in a blackened-bottom watch glass and then viewing the structures through a binocular dissecting microscope with the aid of reflected light. Some of the otoliths from large (older) fish were sectioned with a Buchler, Isomet, 11-1180[7] low-speed saw to facilitate aging. Measurements were not recorded from otoliths since these structures were used only as a method of validating age determined by reading scales.

Lengths by age for fish from all years combined were back-calculated from a scale radius-fish length regression. The regression equation was based on the relationship of magnified (40×) scale length to total fish length. Since a majority of the scale measurements were clustered around a relatively narrow size range, we based our regression on a subsample of scale radius and body length measurements. After grouping the measurements into 25 mm body length intervals, we selected approximately 12 from each interval to ensure that the regression provided good representation. The prediction equation took the form $TL = a\ SR^b$; where TL = total length, SR = scale radius, a = intercept, and b = slope. We substituted the means of the distances from the focus to each annulus for SR in the above equation, calculated the mean fish length for the time of each annulus formation, and then calculated mean growth increment for each age group.

Calculation of a theoretical growth curve is useful in modeling of growth in natural populations of fish. Growth parameters such as theoretical maximum attainable size (L_∞), growth coefficient (K), and theoretical time of the beginning of growth (t_0), may be used in constructing population models. The most popular theoretical growth curve, the von Bertalanffy ($l_t = L_\infty(1 - \exp -K(t - t_0))$) was fitted to back-calculated length at age data (Ricker 1975; Everhart et al. 1975). This particular equation also allows us to make comparisons with results obtained by other researchers.

The growth parameter, L_∞, was first derived by fitting a Walford (1946) line: $l_{t+1} = L_\infty(1 - k) + kl_t$ to back-calculated data where l_t = total length at age t, and k = slope of the Walford line. The slope (k) is equal to e^{-k}, thus our first estimate of $K = \ln k$. Preliminary values of L_∞ were obtained by solving the equation $L_\infty = y$-intercept / $(1 - k)$, and by regressing annual growth increment (X) against fish length at the beginning of the incremental period (Y) (Jones 1976). By plotting $\log_e(L_\infty - l_t)$ against t and by using trial values of L_∞ ranging from lower than the prelimi-

[6]T. Azarovitz, Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, Mass., pers. commun. January 1978.

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

nary values to much greater, we determined the best L_∞ that resulted in the straightest line. The growth coefficient (K) was the slope of this line and was used to solve for t_0:

$$t_0 = \frac{\text{y - intercept of natural log line - } \log_e L_\infty}{K}.$$

We checked the t_0 value to see if it was biased toward younger or older fish by using the equation $t_0 = t(1/K) \ln (1 - l_t/L_\infty)$ for separate ages I-IX (Jones 1976).

Mortality Estimates

We calculated annual total mortality estimates by analyzing catch curves (Beverton and Holt 1957) based on fully recruited age fish and older. If the $\log_e$ of the age frequency in the catch is plotted on age, the slope of the linear descending right limb of the curve is equal to the mean instantaneous total mortality (Z). To calculate mortality rates, we first needed to assign ages to the 1,100 or so unaged fish. We grouped fish of known age by 25 mm length intervals, calculated the percentage of fish of each observed age in each group, and used these percentages to estimate the number of fish of each age for the unaged group (Ricker 1975).

Length-Weight and Fork Length-Total Length Relationships

To calculate length-weight and length conversion relationships fish lengths were subsampled to provide a fairly equal distribution throughout the size range of fish examined during this study. The length-weight relationship was expressed exponentially, whereas the fork length-total length equation was expressed as a simple linear regression.

Spawning

Gonads were examined macroscopically by season to determine the approximate time of spawning. Observations on the development of testes were used collaboratively with measurements recorded from ovaries. Ovaries were weighed to calculate a seasonal gonad index, or the percentage of gonad weight to fish weight.

RESULTS

Distribution and Relative Abundance

Tomtates were collected throughout the South Atlantic Bight (Figs. 1-4). Although most of the continental shelf is sandy "open-shelf habitat" (Struhsaker 1969), the greatest catches of tomtates were directly associated with the irregularly distributed sponge-coral ("live bottom") habitats (as defined by Wenner et al. 1979a). Indices of relative abundance over live-bottom areas were significantly larger ($P<0.01$) than abundance indices from sandy-bottom catches in all seasons and years, except during the cold winter of 1977 (Table 2). Although tomtates occurred in 30-70% of the collections from the sponge-coral habitat, 79.6% of the total number caught during seven cruises, excluding the cold winter of 1977, were at sponge-coral stations (Table 3).

During all seasons, catches of tomtates over sand were infrequent, but occasionally large (Wenner et al. 1979a, b, c, d). Occurrence of tomtates in both sandy-bottom and live-bottom habitats increased the difficulty in biomass estimations. Information from catches over the sponge-coral habitat with the 30-min tows was expanded to preliminary estimates of biomass (Tables 4, 5), although the catch represented a mixed habitat collection of unknown proportions. Standing crop estimates of tomtates from the region between Cape Fear and Cape Canaveral ranged from 1,730 t (minimum catch, summer 1974) to 12,878 t (maximum catch, winter 1976). Although biomass estimates were calculated separately for each depth zone and standing crop estimates were calculated separately for catches from live-bottom and sandy-bottom habitats (Table 6), all estimates represent minimal values because fish availability and vulnerability to the trawl were not considered.

Tomtates, both juvenile (<137 mm TL) and adult, were more abundant in catches in the northern part of the South Atlantic Bight than in catches in the south. During all seasons sampled, between 1973 and 1977, the catch north of lat. 32°32'N, an arbitrary shelf division, was between 59 and 89% of the total catch. The one exception occurred during the cold winter of 1977, when 98% of the total catch (3,192 fish) was made south of lat. 32°30'N at a single station.

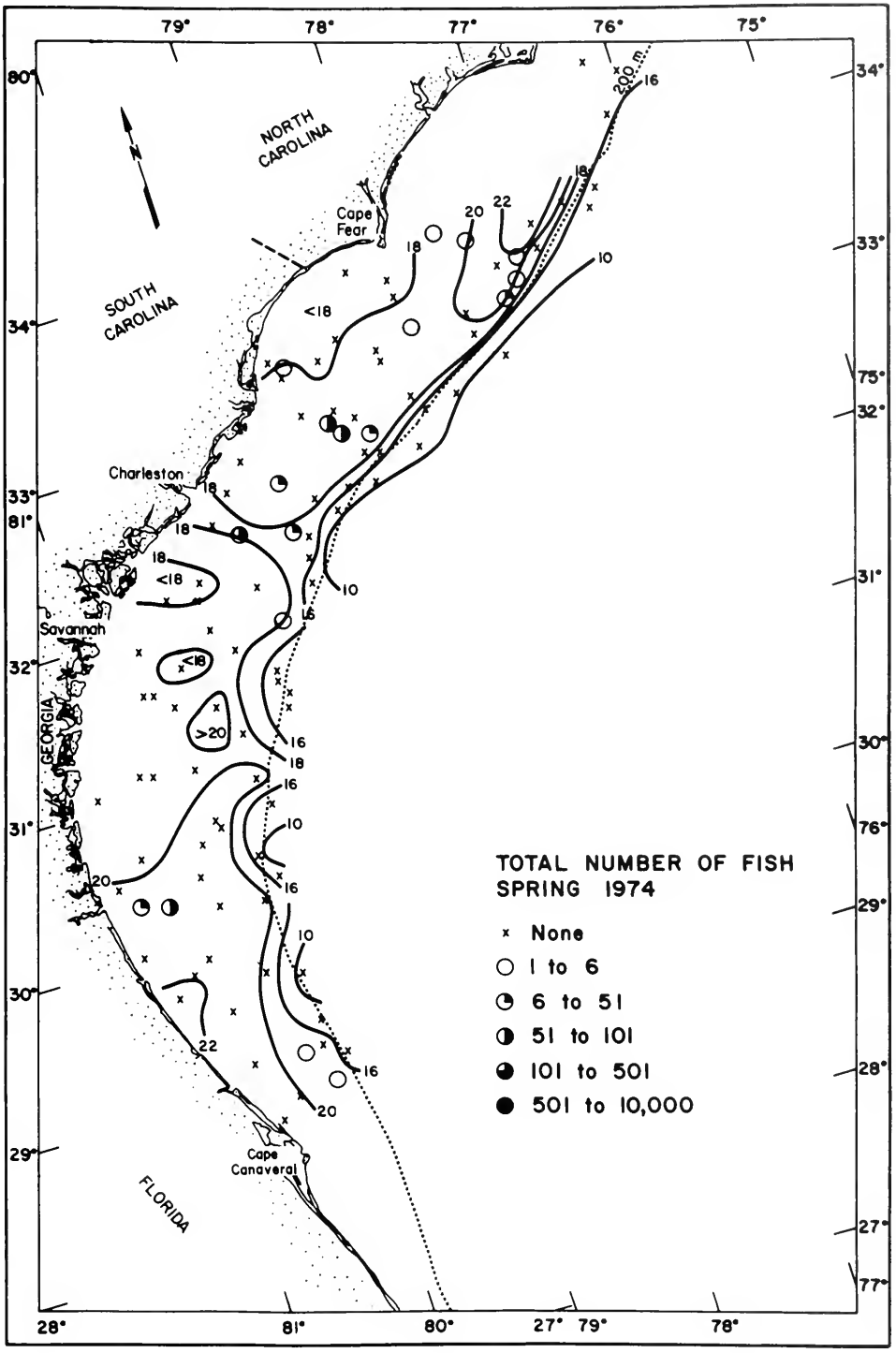

FIGURE 1.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 1 April-9 May 1974.

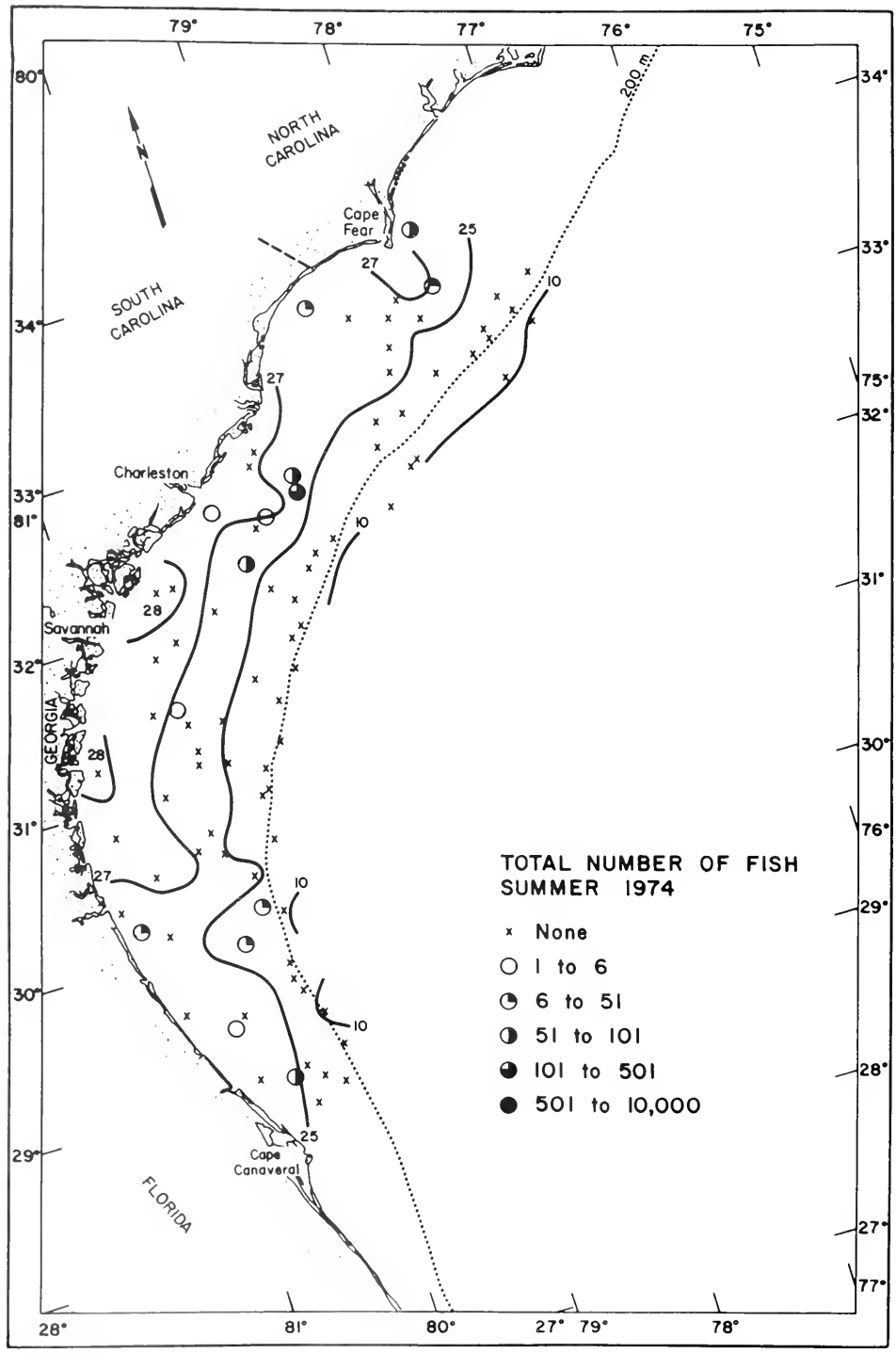

FIGURE 2.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 13 August-19 September 1974.

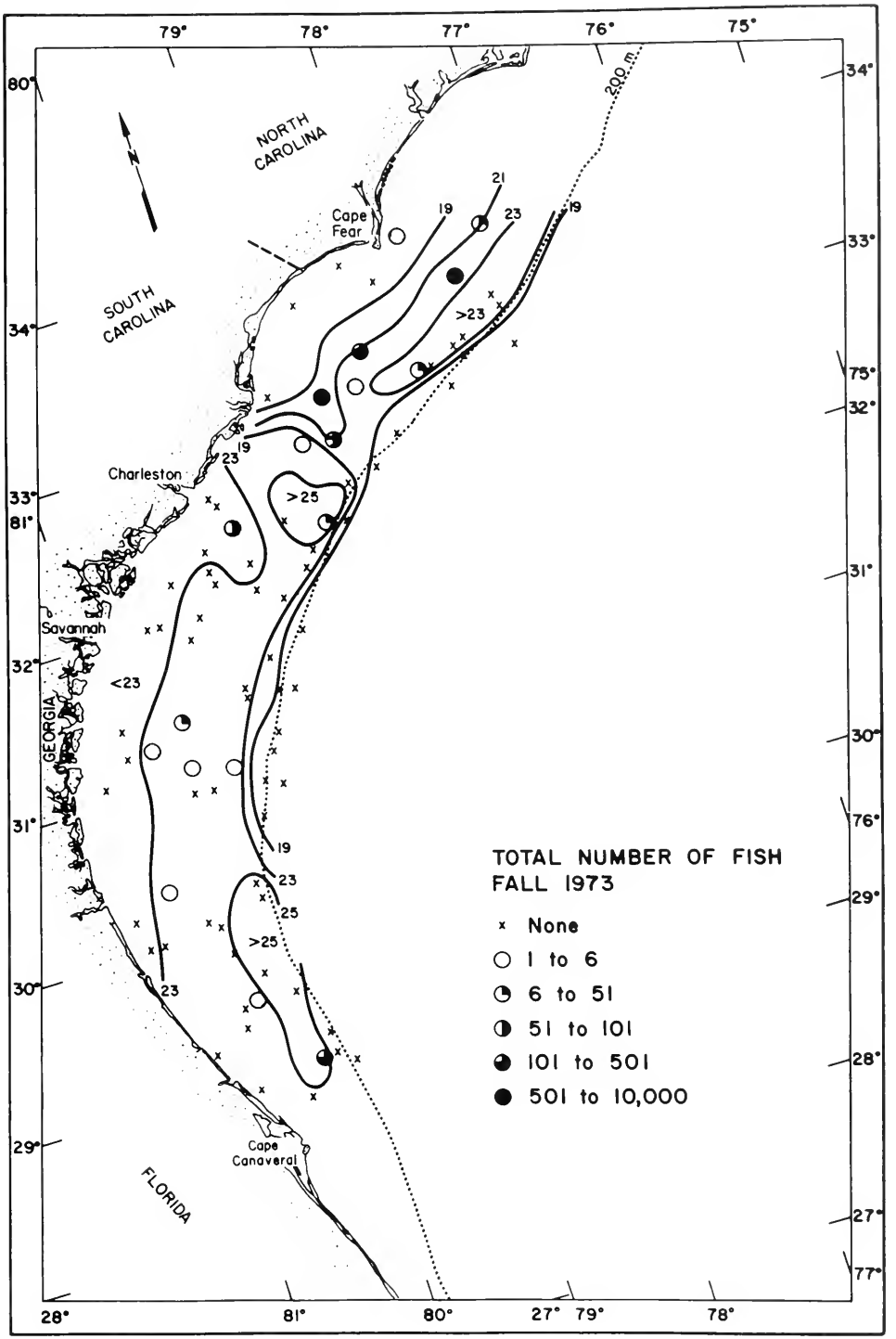

FIGURE 3.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 23 October-16 November 1973.

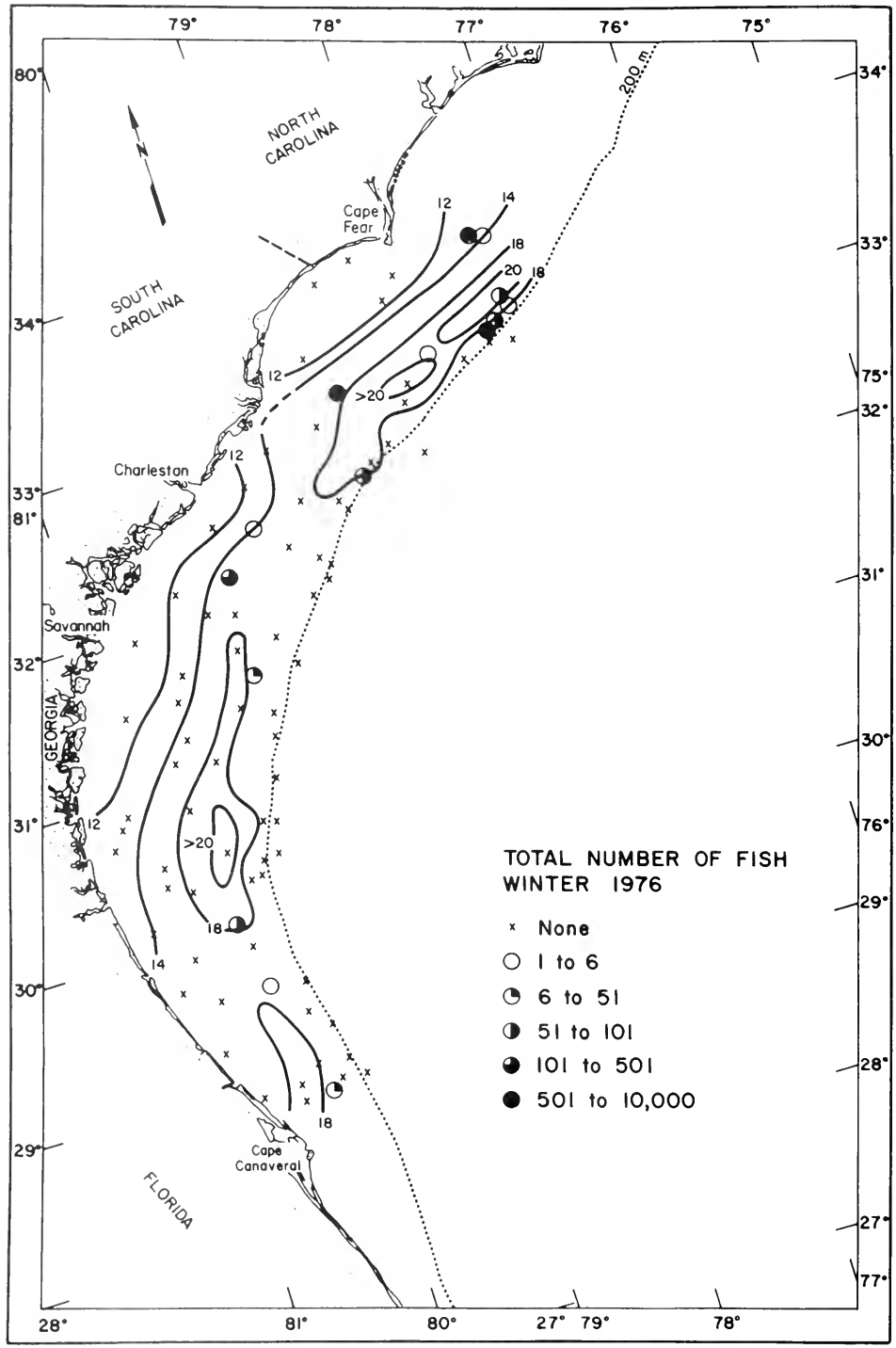

FIGURE 4.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral, 12 January-7 February 1976.

TABLE 2.—*t*-test and chi-square results of comparisons between numbers of tomtates in catches over live-bottom and sandy-bottom habitats.

Seasons	*t*-test of $\frac{\Sigma \ln (x+1)}{n}$	df	χ^2 test of $\frac{\Sigma x}{n}$	df
Fall 1973	3.75**	65	14.79**	1
Spring 1974	4.70**	85	15.69**	1
Summer 1974	4.15**	66	24.73**	1
Winter 1975	2.83**	68	93.36**	1
Summer 1975	8.18**	66	69.46**	1
Winter 1976	8.77**	67	350.41**	1
Summer 1976	11.04**	67	193.32**	1
Winter 1977	1.59n.s.	70	40.42**	1

** = significant at 0.01 level; n.s. = nonsignificant at 0.05 level.

TABLE 3.—Catches of tomtates associated with collections within the "live bottom"-sponge/coral habitats.

Cruise date	Live bottom stations: *N*	Live bottom stations: % with tomtates	Tomtate catch: Total number	Tomtate catch: % from live bottom
Fall 1973	10	39	2,075	29.6
Spring 1974	11	42	442	55.7
Summer 1974	14	50	581	76.2
Winter 1975[1]	9	30	1,212	78.4
Summer 1975	18	70	1,298	98.2
Winter 1976	11	53	4,005	97.6
Summer 1976	8	53	1,749	91.7
Winter 1977[2]	11	55	3,260	1.5
Average		50		79.6

[1]Sampling season prolonged into spring.
[2]Unusually cold winter, data omitted from average.

TABLE 4.—Mean catch/tow ($\bar{y}_h$) values for trawl-caught tomtates on untransformed and transformed [ln (kg + 1)] data by depth and habitat zone for summer 1974. Bliss' (1967) estimation of the mean was applied to the transformed values.

Depth (m)	Habitat	$\bar{y}_h$ biomass (kg/tow) untransformed	$\bar{y}_h$ biomass (kg/tow) transformed	Area of zone (km^2)	No. of tows
9-18	live	5.272	12.981	2,622	2
	sand	0.324	0.163	15,461	14
19-27	live	6.804	6.804	2,730	1
	sand	0.218	0.101	16,100	18
28-55	live	3.991	5.196	3,794	5
	sand	0.000	0.000	22,367	14
56-110	live	1.285	1.120	692	6
	sand	0.000	0.000	4,083	8

TABLE 5.—Mean catch/tow ($\bar{y}_h$) values for trawl-caught tomtates on untransformed and transformed [ln (kg + 1)] data by depth and habitat zone for winter 1976. Bliss' (1967) estimation of the mean was applied to the transformed values.

Depth (m)	Habitat	$\bar{y}_h$ biomass (kg/tow) untransformed	$\bar{y}_h$ biomass (kg/tow) transformed	Area of zone (km^2)	No. of tows
9-18	live	0.000	0.000	2,622	2
	sand	0.000	0.000	15,461	15
19-27	live	104.848	110.616	2,730	3
	sand	0.000*	0.000*	16,100	13
28-55	live	5.450	5.465	3,794	2
	sand	0.133	0.130	22,367	19
56-110	live	2.675	3.163	692	4
	sand	0.001	0.001	4,083	11

TABLE 6.—Minimum standing crop estimates of tomtates in the South Atlantic Bight during summer 1974 and winter 1976. All values should be expanded by 10^2; units are in metric tons. LCL and UCL = lower and upper 90% confidence limits, respectively.

	Untransformed			Transformed		
	Mean($\bar{Y}$st)	LCL	UCL	Mean($\bar{Y}$st)	LCL	UCL
Summer 1974						
sand bottom	3.00	0.02	5.98	2.53	1.05	4.19
live bottom	17.08	7.14	27.02	21.39	8.46	48.36
total area	20.08			23.92		
Winter 1976						
sand bottom	1.05	0.23	1.87	1.02	0.39	1.70
live bottom	108.86	13.39	204.34	127.76	46.71	342.13
total area	109.91			128.78		

Tomtates were collected at depths ranging from 13 to 91 m. The greatest relative abundance of both juveniles and adults in the South Atlantic Bight was consistently within the three shallowest (<55 m) depth zones (Fig. 5). The depth distributions of juveniles and adults indicated a slight shift offshore during winter but did not indicate major seasonal movements of fish within the South Atlantic Bight region. During winters (1975-77), tomtates were not collected in the nearshore (9-18 m) zone. In summer 1976, only adults were caught in the deep 56-110 m depth zone. During fall 1973 and winter 1977, only juveniles were collected in the 56-110 m depth zone, while in winter 1976, juveniles were much more abundant than adults in this depth zone.

Tomtates were collected at bottom temperatures from 10.3° to 28.1°C, but were seldom caught at temperatures <13°C. Differences in thermal distributions of juvenile (≤148 mm TL) and adult tomtates in the South Atlantic Bight indicated separate thermal preferences. During fall (1973) and winter (1976), the proportion of juveniles to adults in the total catch increased at

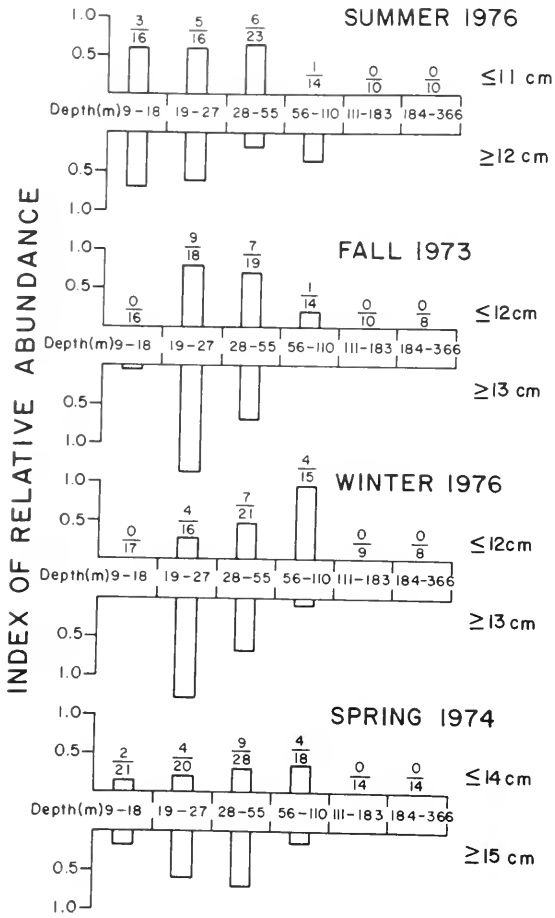

FIGURE 5.—Index of relative abundance for tomtates by depth zone during four seasons (juveniles above the axis, adults below: fraction numerator = number of trawls with tomtates; denominator = total number of trawls in depth zone).

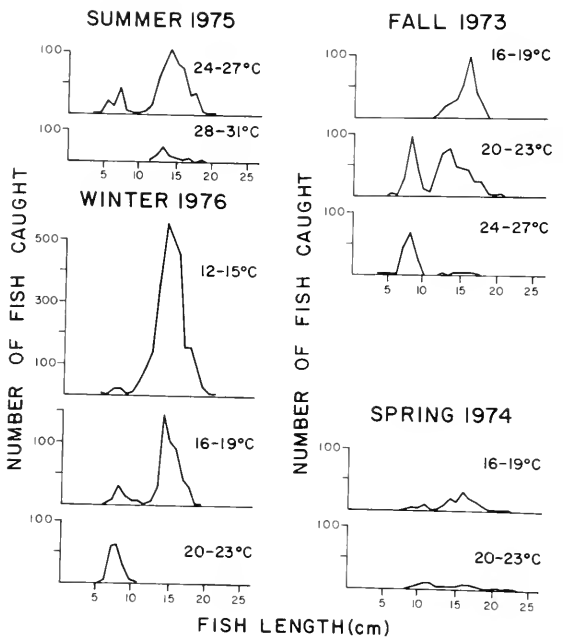

FIGURE 6.—Length-frequency distributions (TL) of tomtates by bottom water temperature interval (4°C).

higher temperature intervals (Fig. 6). Young tomtates (20-63 mm) have previously been collected during December in the Florida Keys at a water temperature of 16.2°C (Springer and Woodburn 1960). During summer (1975), juveniles were collected only in the coolest thermal zone (24.0°-27.9°C), while during spring (1974), both juveniles and adults were collected in the same thermal interval (16.0°-23.9°C).

Tomtates may avoid water temperatures of <10°C. Fish were never caught at <10.3°C during any season, even at five sponge-coral stations in areas where large numbers were caught at >10°C during the previous winter (Fig. 7).

Age and Growth

Validity of Rings as Annuli

Both scales and otoliths were used to age tomtates. Approximately 75% (397 of 529) of the scale samples and 85% (177 of 208) of the otoliths were legible. Since tomtates have been aged by reading scales (Sokolova 1969), we did not try specifically to validate the methods presented here. Several findings, however, pursuant to the goals of this paper, indicate that rings on tomtate scales and otoliths are true annuli. Close examination of otoliths from young-of-year tomtates, collected by trawl, clearly show the formation of one ring per year, and that the first ring (annulus) forms between the fall and spring collection periods.

The mean length of fish progressively increased as the number of scale or otolith rings increased and otoliths and scales agreed closely (Table 7). For instance, if aged by scales, age-I fish averaged 135.4 mm TL; age-II, 181.9; age-III, 203.3; age-IV, 220.0; age-V, 234.5; age-VI, 255.7; and age-VII, 265.8. If aged by otoliths, age-I fish averaged 134.3 mm TL; age-II, 164.7;

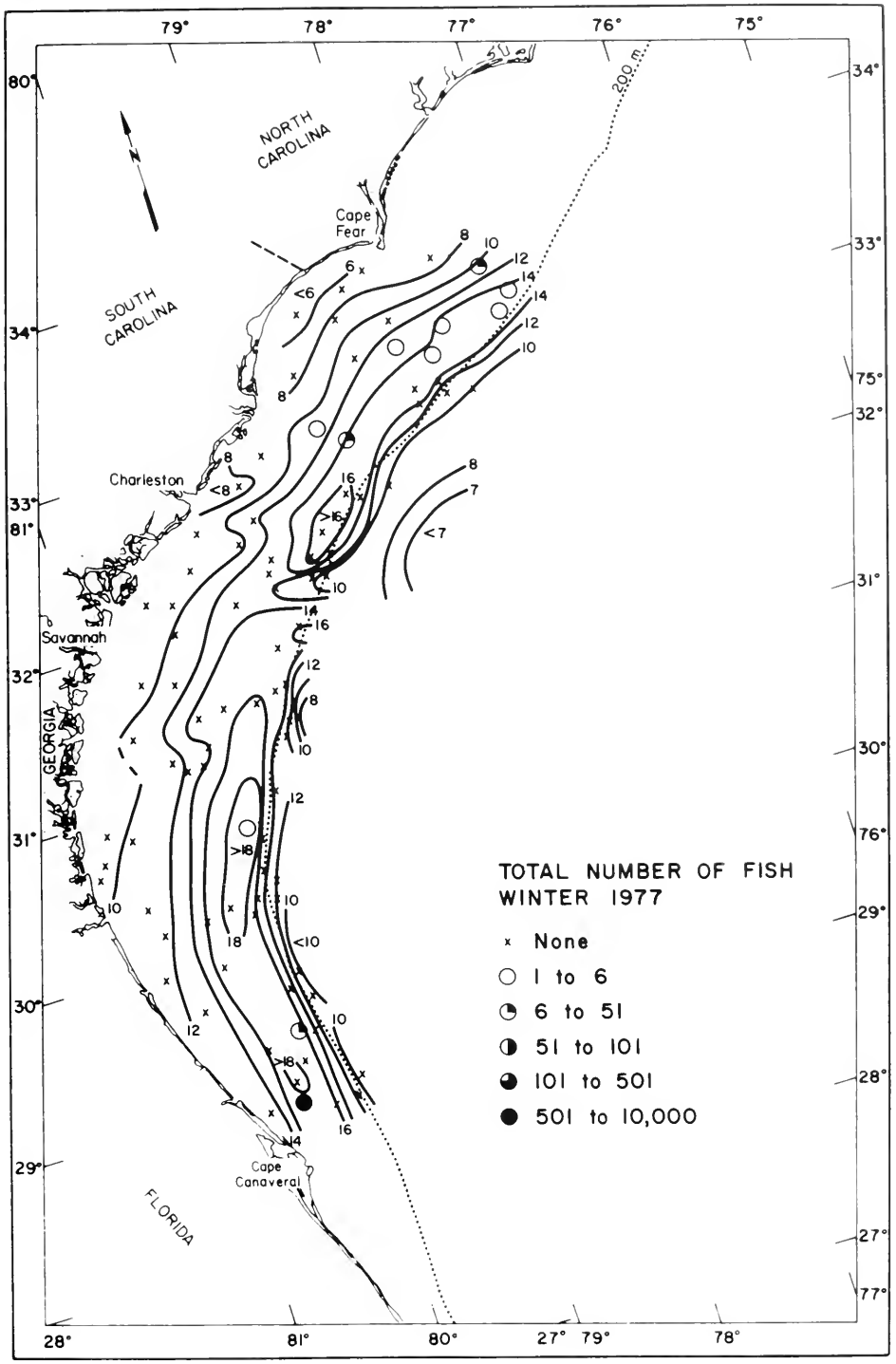

FIGURE 7.—Spatial distribution and catch per tow of tomtates between Cape Fear and Cape Canaveral during the cold winter of 1977.

TABLE 7.—Comparison of mean empirical length-age data obtained by reading tomtate scales and otoliths.

	Scales				Otoliths				
Age group	N	Mean TL (mm)	Range in length (mm)	SD	N	Mean TL (mm)	Range in length (mm)	SD	Difference in means (mm)
0	22	84.7	50-142	28.1	54	89.8	50-142	29.9	5.1
1	9	135.4	109-171	25.6	23	134.3	80-157	21.5	1.1
2	45	181.9	153-206	13.3	43	164.7	150-185	9.7	17.2
3	81	203.0	180-221	9.6	16	197.1	161-212	14.7	5.9
4	134	220.0	195-238	10.5	19	213.0	193-227	11.1	7.0
5	66	234.5	208-257	11.3	12	232.2	226-242	4.1	2.3
6	28	255.7	245-268	6.3	9	253.1	240-262	6.5	2.6
7	5	265.8	260-272	5.5	1	267.0	—	—	1.2
8	4	277.0	270-280	5.0					
9	3	286.7	282-289	4.0					
Total	397								

age-III, 197.1; age-IV, 213.0; age-V, 232.2; age-VI, 253.1; and age-VII, 267.0 mm.

The relative length frequencies of the measured distance from the focus of the scale to each ring progressively increased with the number of rings. Significant features of the plotted curves were the occurrence of one mode for each ring, the consistent location of a specific mode on the X-axis for fish of different ages, the increased overlap for each additional ring, and the progressive decrease in the distance between modes for each successive year, indicating less linear growth each year as the fish ages.

Growth

There was relatively little difference in the mean annual increments of fish aged by scales and those of fish aged by otoliths (Table 7). Annual growth increments for fish aged by scales for ages I-V were: I-II, 46.5 mm; II-III, 21.1 mm; III-IV, 17.0 mm; and IV-V, 14.5 mm. After age V, growth appears to be more irregular, probably a result of the relatively small sample sizes for ages VI, VII, VIII, and IX (Table 7).

Lengths by age for fish from all years were back-calculated from a scale radius-fish length regression. The prediction equation was

$$TL = 1.7489\ SR^{0.9572};\ r = 0.93 \text{ and } N = 103,$$

where TL = total length, and SR = scale radius. By substituting the means of the distances from the focus to each annulus for SR in the above equation, we were able to calculate the mean fish length at the time of each annulus formation, and the mean annual growth increment for each age (Table 8).

The von Bertalanffy equation was used to describe theoretical growth. The growth parameters L_∞ and K were first calculated by fitting a Walford (1946) line to back-calculated data. The equation was $l_{t+1} = 90.833 + 0.6747_{l_t}$, $r = 0.982$. Our first estimate of K was l_n 0.6747 or 0.3935. This value was used to obtain L_∞ by solving the equation $L_\infty = y\text{-intercept} / (1 - k)$. The initial value for L_∞ of 289, and the subsequent value of 285.7 obtained by regressing annual growth increment (X) against fish length at the beginning of the incremental period (Y) (Jones 1976),

TABLE 8.—Calculated total lengths (millimeters) of 346 tomtates aged by scales.

Observed age	N	Mean calculated total length at end of year								
		1	2	3	4	5	6	7	8	9
I	9	103.7								
II	45	108.1	173.0							
III	75	102.5	171.1	199.1						
IV	123	102.6	168.4	198.8	214.1					
V	56	101.0	167.8	200.7	216.7	226.7				
VI	26	102.2	165.5	198.8	221.1	235.7	245.1			
VII	5	99.6	165.3	200.9	224.4	240.8	251.3	258.8		
VIII	4	105.3	171.7	195.5	215.1	228.6	242.0	252.1	260.8	
IX	3	102.5	170.6	200.9	222.1	237.7	253.0	264.5	273.5	280.5
Total	346									
Weighted mean		103.0	169.3	199.3	216.0	230.4	246.2	258.0	266.2	280.5
Increment		103.0	66.3	30.0	16.7	14.4	15.8	11.8	8.2	14.3
No. calculations		346	337	292	217	94	38	12	7	3

seemed low. Therefore, we plotted $\log_e (L_\infty - l_t)$ against t by using trial values of L_∞ ranging from 285 to 310 mm. The straightest line resulted from L_∞ of 310 mm. The slope of the line, −0.22017, was selected as the growth coefficient (K) and was used to obtain t_0 (−1.28). Our best estimate of the equation describing the theoretical growth of tomtates is

$$l_t = 310\,(1 - \exp - 0.22017(t + 1.28)).$$

Observed, back-calculated, and theoretical lengths at age are presented in Table 9.

TABLE 9.—Total lengths of tomtates at age (observed, back-calculated, and theoretical).

Age	Length at age (mm)		
	Observed	Back-calculated	Theoretical
1	135.4	103.0	122.4
2	181.9	169.3	159.4
3	203.0	199.3	189.2
4	220.0	216.0	213.1
5	234.5	230.4	232.2
6	255.7	246.2	247.6
7	265.8	258.0	259.9
8	277.0	266.2	269.8
9	286.7	280.5	277.8

Mortality Estimates

By age IV, tomtates are fully recruited to the hook and line fishery, the only important method of harvesting this species off the southeastern United States. Instantaneous mortality (Z) estimates were obtained by analyzing catch curves of fish aged IV and older (Fig. 8). The mean total annual mortality estimate for 1972 through 1978 was 59% ($Z = 0.887$). By year, instantaneous mortality rates were 1974, 0.669; 1975, 1.035; 1976, 1.017; 1977, 1.041; and 1978, 0.972. Too few fish were sampled from the fishery in 1972 and 1973 to construct catch curves. The instantaneous mortality rate(s) for tomtates was higher than those previously obtained for white grunt, $Z = 0.65$ (Manooch 1976), or for red porgy, $Z = 0.58$ (Manooch and Huntsman 1977).

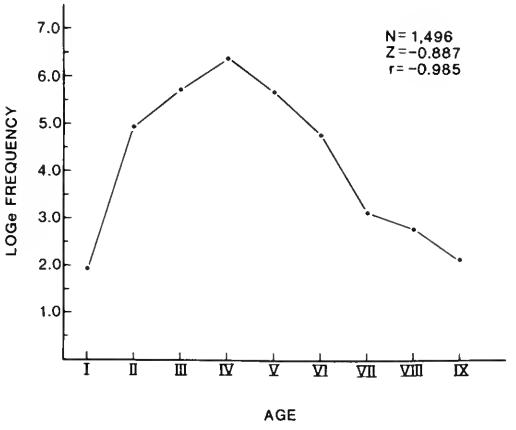

FIGURE 8.—Catch curve for tomtates caught by hooked line off the southeastern United States, 1974-77.

Length-Weight and Fork Length-Total Length Relationships

Fish ranging from 52 to 280 mm TL were used to calculate a length-weight relationship. The equation

$$W = 0.0000086L^{3.0905},\ r = 0.996 \text{ and } N = 70,$$

where W = weight in grams and L = total length in millimeters, describes this relationship. The equation $TL = -1.8196 + 1.1540\ FL$, $r = 0.99$ and $N = 100$ was derived to convert lengths.

Spawning

Indirect evidence indicates that tomtates of the South Atlantic Bight spawn primarily in April and May. Running ripe males and partly spent females were caught in April 1979 (28-42 m; 16.4°-19.4°C), while a major decrease in mean ovarian weight and maximum ovary weight of mature females occurred after the spring (April 1974) sampling period (Table 10). Throughout the year, many (>38%) of the females sampled each season were in the maturing and ripe condition. The presence of juveniles (33-90 mm TL; mode 80 mm) in bottom trawl collections during summer, and the progressive increase in modal fish lengths in length-frequency distributions

TABLE 10.—Gonad condition of adult tomtates (>15 cm TL) from the South Atlantic Bight.

Season	Sex	N	Running ripe %	Mean ovarian wt. (g)	Gonad index[1]	Maximum ovarian wt. (g)
Summer 1974	F	31	5	0.6	0.6	1.7
Fall 1973	F	48	2	0.5	0.5	1.4
Winter 1976	F	36	9	1.3	1.1	8.6
Spring 1979[2]	M	13	77	—	—	—
	F	34	0	4.2	3.4	17.0

[1]Gonad index = (ovary wt./fish wt.) × 100.
[2]Females 77% with hydrated eggs.

through a seasonal cycle (Fig. 9), indicated that these juveniles were spawned in spring.

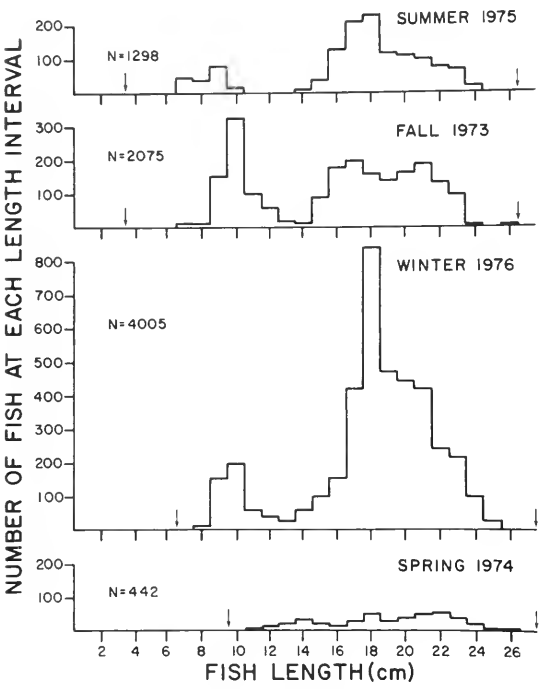

FIGURE 9.—Length-frequency distributions (FL) from the total catch of tomtates between Cape Fear and Cape Canaveral during each of four seasons.

DISCUSSION

Distribution and Abundance

Tomtates are considered abundant in several habitats in and to the south of the South Atlantic Bight, and indicate daily movements between habitats. Within the Bight, tomtates were common over both live-bottom and shelf-edge habitats during earlier (1959-64) exploratory fishing (Struhsaker 1969). Farther south, tomtates were found over broad sandy areas off southern Florida (Craig 1976), near coral stacks in the Tortugas Islands (Longley and Hildebrand 1941), and in grass beds and other open areas in the Bahamas (Bohlke and Chaplin 1968). Tomtates were common from nearshore to the offshore reefs in Florida and were abundant on the shrimp grounds of the Dry Tortugas and the Gulf of Mexico (Courtenay 1961). In the Virgin Islands, changes in distribution with respect to habitat type were associated with feeding behavior. Tomtates feed as individuals or in small schools at night over open sand (Collette and Talbot 1972), and they spend the day on the reef segregated into size groups; juveniles school over the highest part of the reef, while adults hover low between the coral colonies (Smith and Tyler 1972).

Juvenile tomtates may occur in several habitats, either inshore or offshore, which include "live bottom" and rocky outcrops similar to those occupied by adults. Small tomtates (≈33 mm) were abundant over artificial reefs (Parker et al. 1979) and natural ridges in spring through fall off the Carolinas and have been found in the mouths and stomachs of black sea bass in the same areas (Parker[8]). Young tomtates also frequent grass beds (Randall 1968), subtidal mud flats (Reid 1954), and nearshore areas around wharfs (Jordan and Evermann 1896). The presence of young fish among spines of sea urchins (Johnson 1978) suggests that microhabitats may be important to the survival of some early life stages. Juveniles of French grunts, *H. flavolineatum*, and white grunts, *H. plumieri*, form large multispecies schools closely associated with particular coral formations (microhabitats) during the day and follow precise routes (≥100 m) to and from feeding areas (sea grass beds) at night (Ogden and Ehrlich 1977).

Biomass and standing stock calculations for tomtate from groundfish trawling were considered preliminary, minimal estimates. More satisfactory estimates should incorporate information on 1) abundance/biomass sampling conducted completely within a known area of a given habitat type, 2) the correct proportional allocation of a day/night catch factor for each habitat sampled, 3) the vulnerability of tomtate to the sampling gear, and 4) estimates of biomass from untrawlable, rocky outcrop, habitats. Unfortunately, none of the above information is available at present, so our estimates were based upon continuous day/night sampling imposed on the very random nature of sponge-coral habitat distribution. Discrete, short duration trawling completely within the boundaries of the patchy sponge-coral habitats could be directed by pretrawl bottom mapping with underwater TV

[8]R. O. Parker, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516, pers. commun. January 1978.

(Powles and Barans 1980). This method would allow more accurate quantification of relative abundance differences between habitats and between day and night sampling. Then, a biomass factor could be developed to proportion fish availability to the trawl during daytime collections in sponge-coral habitats and during night in sand bottom habitats. Also, the vulnerability of tomtate, or any groundfish in the South Atlantic Bight, to trawl gear is unknown. Several experiments with a headrope mounted TV system would do much to fill this data gap. Biomass estimates from rocky habitats may have to be extrapolated from nearshore diver counts or offshore TV counts, but many problems remain in the interpretation of these data. In general, a composite estimate of tomtate biomass or standing stock in the South Atlantic Bight should include difficult to obtain fish behavior information.

Tomtate are relatively shallow water (<50 m) groundfish with a more pronounced tendency for annual depth migrations in populations south of the South Atlantic Bight. Tomtates in the Campeche Bank area were most abundant in waters <30 m during all seasons (Sauskan and Olaechea 1974), while tomtates occurred only at depths of <10 m in the Bahamas (Bohlke and Chaplin 1968). Although tomtates remain inshore during winter in Florida (Courtenay 1961), they are not caught by inshore shrimp trawlers off South Carolina (Keiser 1976) and appear to avoid shallow waters (<20 m) north of Florida during winter. There is the possibility that during extremely cold winters, slight migrations (shifts in distribution) southward occur.

In contrast to the results of this study, tomtates of the Campeche Bank move onshore during winter and fall and offshore in spring and summer and are recruited to the fishery in shallow waters, a great distance from the deeper area where spawning takes place (Sauskan and Olaechea 1974). The difference in location of spawning and recruitment and lack of large adult fish over reefs in Florida (Stone et al. 1979) and in commercial trawl catches (Sokolova 1969) suggests separation of juvenile and adult populations, especially south of Florida.

Age and Growth

The fact that scales may be used to accurately determine the age of a warmwater marine fish species is not particularly surprising. Scales have been used to age other reef fishes that occur with tomtates in the South Atlantic Bight. Manooch (1976) found annuli on scales from white grunt collected off the Carolinas; Manooch and Huntsman (1977) aged red porgy, *Pagrus pagrus*, using both scales and otoliths; and Grimes (1978) determined the age of vermilion snapper, *Rhomboplites aurorubens*, by reading scales.

The theoretical parameters derived in this study are compared with those for tomtates from the Campeche Banks, and with cooccurring species in the South Atlantic Bight in Table 11. The Campeche Banks fish did not live as long—5 or 7 yr compared with 9 in the South Atlantic Bight—and had a slightly smaller maximum size (L_∞), 295 mm compared with 310 mm. Consequently, the growth coefficient, although very similar, is slightly higher—0.235 compared with 0.200. With the exception of black sea bass, *Centropristis striata*, sympatric species previously studied in the South Atlantic Bight were longer lived and slower growing (Table 11).

TABLE 11.—Growth parameters for six species of demersal fish.

Common name	Scientific name	Area	Author	M	K	L_∞ (TL, mm)	Longevity (yr)
Tomtate	*Haemulon aurolineatum*	N.C., S.C., Ga., east coast Florida	This paper		0.22017	310	9
		Campeche Banks	Calculated from Sokolova (1969)		0.235	295	5
			Sauskan and Olaechea (1974)				7
White grunt	*H. plumieri*	N.C., S.C.	Manooch (1976)	0.4 & 0.6	0.108	640	13
Red porgy	*Pagrus pagrus*	N.C., S.C.	Manooch and Huntsman (1977)	0.2	0.096	763	15
Vermilion snapper	*Rhomboplites aurorubens*	N.C., S.C.	Grimes (1976)	0.25	0.198	627	10
Gag	*Mycteroperca microlepis*	N.C., S.C., Ga., east coast Florida	Manooch and Haimovici (1978)	0.20	0.121	1,290	13
Black sea bass	*Centropristis striata*	N.C., S.C.	Mercer[1]	0.30	0.220	352	8

[1]Linda Mercer, Virginia Institute of Marine Sciences, Gloucester Point, Va.

Spawning

Growth rates of juvenile tomtates (≥130 mm TL/first year) in the South Atlantic Bight and rates estimated from larvae of similar species support the spawning season indicated by analysis of gonads. If growth of very early stages of tomtates approximates the 14 mm SL/30 d for white grunts (Saksena and Richards 1975) and French grunts (Brothers and McFarland In press), tomtates of 30-90 mm TL caught in early September may have been spawned between early April and June. Identification of peak spawning period of tomtate by associated larval abundance was impossible due to difficulties in identifying larval haemulids.

Populations of tomtates farther south appear to have a prolonged spawning season. Munro et al. (1973) reported collections of ripe females between January and August in Jamaica, while Cervigon (1966) suggested that tomtates spawn throughout the year in Brazil. Tomtates from Campeche Bank spawn primarily during July-September at depths of >50 m and again during winter at shallower depths (Sauskan and Olaechea 1974).

Management

We believe management of the tomtate fishery should be considered for three reasons. First, the species is easily captured by a variety of fishing techniques: hook and line, trap, and unlike most other reef fishes, by trawl. Second, fishing effort applied to this, and other associated, species will probably increase. And third, the tomtate is a member of a rather delicate faunal community and is a major source of food for higher trophic level, piscivorous fishes. Unwise harvest of one species could have both physical and energetic impacts on the community as a whole.

While regional catches of tomtates may at times be quite large, for instance by recreational anglers on headboats fishing inshore waters, the species ranks low in terms of poundage landed in the South Atlantic Bight by both recreational and commercial fishermen. Because tomtates are small and not competitive in value with other reef fishes in the commercial market, commercial hook and line fishermen usually discard the species or use it as bait for larger predatory fishes, such as groupers and snappers (Wenner[9]).

Given the geographical range of *H. aurolineatum*, its abundance as indicated by exploratory trawling, and relatively low harvest by fishermen, one could label it as an "underutilized species" in the South Atlantic Bight. However, assigning tomtates this status requires a thorough understanding of currently operating fisheries plus a knowledge about the role of the species in the ecosystem. We do not recommend such a designation at this time.

Although the distribution of tomtate is continuous from the southeastern coast of the United States to the Campeche Banks, the stock fished in each area should be considered separate for assessment and fishery management. Our study and the studies of Sokolova (1969) and Sauskan and Olaechea (1974) show that tomtates are a relatively short-lived, fast-growing reef fish with a high annual mortality rate when compared with other reef fishes of the region. Fish with these biological traits usually are not as readily overfished as those that grow more slowly, those that live longer, and those with a lower annual mortality rate. However, many fast-growing, high-mortality species such as mackerels (*Scomberomorus*), some tunas (*Thunnus*), and menhaden (*Brevoortia*), which are important to large fisheries, have demonstrated some signs of being overfished.

By comparing our study with those on the Campeche Bank, we can look at one stock caught at present primarily by hook and line and the other by a more intensive gear, the trawl. The major difference between the South Atlantic Bight tomtates and those from Campeche Bank is that the Atlantic stock is older and larger. There are several explanations other than biological changes in ecology or genetics for the differences between these stocks. In our study, the tomtates were caught by recreational fishermen using hook and line while those from Campeche Bank were trawled. Hook and line fishing may be more selective of larger fish and some of the smaller fish may be discarded by the fishermen resulting in larger fish of each age being sampled. A more likely explanation is that the large, old Atlantic fish have a generally low exploitation rate. The Soviet-Cuban trawlers have fished Campeche Bank since 1964 with catches of grunts averaging over 20,000 tons a year and ex-

[9]C. A. Wenner, South Carolina Wildlife and Marine Resources Department, Marine Resources Research Institute, Charleston, SC 29412, pers. commun. January 1978.

ceeding 60,000 in 1971 and 1975 for the region according to FAO Yearbooks. If, as we suspect, most of these catches were tomtate, the Campeche stock has been much more exploited than the Atlantic for the past 10 yr.

Regional harvest of tomtates by hook and line will probably remain low. Recreational anglers will continue to catch small numbers, and commercial handliners will continue to regard *H. aurolineatum* as "trash fish" or bait. Any increase in the harvest will probably involve an expansion of a trawl fishery off South Carolina, Georgia, and northeast Florida.

Prior to development of any U.S. groundfish trawl fishery for tomtate, the possibility of habitat destruction by trawl gear should be investigated. Some bottom trawl harvest techniques may have detrimental effects on the substrate community in which tomtate are most abundant. Destruction or removal of the sponge/coral invertebrates and crab species, or damage to *Oculina* coral beds, may indirectly reduce future yields of tomtate and other fish species.

Also, during several seasons trawls may catch juveniles of a species important to both commercial and sport fisheries prior to their recruitment to harvest by hook and line. Bottom trawling for tomtate in "live bottom" areas would catch large numbers of small, commercially unimportant fish species and invertebrates which would increase costs of sorting unless the entire catch was processed as a mixed species product.

In our study the greatest relative abundance (catch/tow) of adults was during winter at which time commercial harvesting could take advantage of any concentrations of fish resulting from a shift to a more offshore distribution of the population. Reduction of fishing effort during late winter and early spring would allow the unfished stock to spawn and juveniles to be recruited to the fishery at a larger size, possibly regulated by net mesh size. Even in this case, a drastic reduction in population size could adversely affect the recreational headboat fishery.

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GROWTH OF THE OCEAN QUAHOG, *ARCTICA ISLANDICA*, IN THE MIDDLE ATLANTIC BIGHT

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ABSTRACT

In situ growth rate of the ocean quahog, *Arctica islandica*, was investigated at a site 53 m deep off Long Island, New York, during 1970-80. Specimens notched during summer 1978 and recaptured 1 and 2 calendar years later yielded information on shell growth and the periodicity of supposed annual marks. Growth of specimens recaptured after 1 year at liberty ($n = 67$, 59-104 mm shell length) was described by $SL_{t+1} = 2.0811 + 0.9802\ SL_t$, where SL is shell length in millimeters at age t. Average shell length of marked specimens recaptured during summer 1980 increased 1.17 mm ($n = 200$), approximately twice that of ocean quahogs recaptured in 1979 (0.56 mm). Band formation on the external surface of small ocean quahogs (less than about 60 mm) was apparently an annual event since small specimens recaptured in 1979 formed one such mark during the interval between release and recapture. Small specimens sampled during summer exhibited relatively wide marginal growth from the last external mark to the shell edge, while winter samples had formed new annuli at the shell margin, thus, external bands were formed during early autumn-early winter. Internal banding in shell cross sections of small ocean quahogs correlated in number and position with external features. An equation representing back-calculated growth, based on external banding patterns of small unmarked specimens (19-60 mm) captured during summer 1978, was: $SL = 75.68\text{-}81.31\ (0.9056)^t$, where t is age in years. Length-frequency samples were available for the vicinity of the marking study from routine dredge surveys of clam resources during 1970-80. Growth rates inferred from progressions of length-frequency modes in 1970 and 1980 samples were similar to those computed from mark-recapture and age-length equations. Ocean quahogs are apparently among the slowest growing and longest lived of the continental shelf pelecypods; annual increases in shell length were 6.3% at age 10, 0.5% at age 50, and 0.2% at an estimated age of 100 years.

Research on the population dynamics of the ocean quahog, *Arctica islandica*, has become increasingly important in recent years. An intensive fishery for the species developed off New Jersey and the Delmarva Peninsula during the mid-1970's. The resulting increases in U.S. landings were dramatic: from 588 t of shucked meats in 1975 to a record 15,748 t by 1979. Estimates of the growth rate and longevity of ocean quahogs inhabiting the Middle Atlantic Bight are necessary to assess potential impacts of various harvesting strategies on the resources (Murawski and Serchuk[2]; Mid-Atlantic Fishery Management Council[3]).

Several early studies alluded to the age and growth rate of *Arctica islandica*, yet citations were largely anecdotal and generally did not reflect critical evaluations of the rate of growth or the validity of aging criteria. Turner (1949) reported an observation by G. Thorson that "European investigators who have studied the chemical composition of the shell found reason to believe that it took six years or more for mahogany (ocean) quahaugs (quahogs) to reach average size." Loosanoff (1953) stated that ocean quahogs he examined for reproductive studies "were adults, several years old, and averaged 3½ to 4 inches (89-102 mm) in length." Jaeckel (1952) noted *Cyprina* (=*Arctica islandica*) could perhaps attain ages up to 20 "Sie kann hohes Alter (Vielleicht bis zu 20 Jahven) erreichen." Skuladottir[4] did not elaborate on aging methodologies

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Murawski, S. A., and F. M. Serchuk. 1979. Distribution, size composition, and relative abundance of ocean quahog, *Arctica islandica*, populations off the Middle Atlantic Coast of the United States. ICES/C.M. 1979/K:26, Shellfish Comm., 22 p.

[3]Mid-Atlantic Fishery Management Council. 1979. Amendment No. 2 for the surf clam and ocean quahog fishery management plan and final supplemental environmental impact statement. Mid-Atlantic Fishery Management Council, Dover, Del., 114 p.

[4]Skuladottir, U. 1967. Kraffadyr og skeldyr (Crustacean and mollusks). Radstefna Isl. Verkfraedinga. 52:13-23.

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but claimed "the oldest clams were up to 18 years and about 9 cm long. The bulk was in the 10-14 year group and 7-8.7 cm long."

The external color of large ocean quahogs (greater than about 60 mm shell length) is usually solid black; however, the periostracum of small individuals is variable in color, grading from pale yellow to deep brown (Lovén 1929; Hiltz[5]). Concentric dark bands appearing in the shell surface of small specimens have thus been interpreted as annuli by several authors. Although Lovén did not present age-size relationships explicitly, he did note the presence of external "annual rings" ("Jahresringe") and presented photographs of a size range of small ocean quahogs, illustrating the relationship between numbers of rings and shell lengths. Chandler[6] measured the maximum diameters of concentric rings and derived growth relationships based on eight specimens (96 total measurements, to millimeters). The largest number of such rings appearing on an individual ocean quahog was 21; the corresponding shell length was 58.5 mm. Caddy et al.[7] presented growth curves, based on external markings, for small ocean quahogs from the Northumberland Strait and Passamaquoddy Bay. Average length at age was consistently greater for the more southern area.

Unpublished manuscripts by Chéné[8] and Meagher and Medcof[9] document efforts to more precisely establish ocean quahog growth rates. Mark and recapture experiments were conducted in Brandy Cove, New Brunswick. Notched specimens ($n = 14$), averaging 57.4 mm (shell length) when recaptured, grew an average of 0.6 mm (shell height) between September 1970 and September 1971. Sequential observations of eight small ocean quahogs (mean length 20.16 mm) was undertaken to assess growth rates and seasonal changes in the color patterns of the periostracum. These individuals were held in cages and grew an average 17% in length from 4 June to 31 August 1971. Periostracum formed during the interval was brown, contrasting with yellow material formed before the study was begun. However, this banding pattern may not have been indicative of a normally occurring annual event since "the caged clams were sensitive to experimental treatments and produced disturbance rings each time they were air-exposed for observation" (Meagher and Medcof footnote 9).

Several recent studies have examined banding patterns present in shell cross sections and have attempted to validate the hypothesis of band formation as an annual event. Jones (1980) noted that marginal increments of shell deposition beyond the last band followed a seasonal progression; bands were formed once per year between September and February. The most rapid production of shell was from late spring to early summer; annulus formation overlapped the spawning period in mature individuals. Thompson et al. (1980) presented size-frequency data of small specimens from the Baltic Sea and interpreted external and cross-sectional banding in these specimens as supporting evidence for annual periodicity of band formation in larger (older) specimens from the Middle Atlantic Bight. Thompson et al. further stated that preliminary results from radiochemical analysis of shells corroborated age analysis based on shell banding patterns.

We initiated a project during summer 1978 to assess in situ growth rates of ocean quahogs at a deepwater site off Long Island, N.Y. Objectives of the study were to obtain growth increment data directly from mark-recapture, further evaluate the potential of banding patterns (both external and in shell cross section) as indicators of age, and correlate growth measurements with a 10-yr time-series of length frequencies collected in the vicinity of the marking site. Length-weight relationships have been established for the Middle Atlantic, based on a synoptic winter survey (Murawski and Serchuk 1979); however, no data have been published on seasonal variations. An additional objective of the project was to compare winter and summer length-weight relations at the marking site.

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FIELD STUDIES

Intermittent surveys of offshore clam resources of the Middle Atlantic Bight have been conducted since 1965 by the National Marine Fisheries Service, and its predecessor the Bureau of Commercial Fisheries (Merrill and Ropes 1969; Murawski and Serchuk footnote 2; Serchuk et al.[10]). Cruises were designed to yield information on temporal and areal aspects of distribution, size composition, and relative abundance of both surf clam, *Spisula solidissima*, and ocean quahog. Stations were sampled in a grid array prior to 1978; surveys from 1978 to 1980 employed a stratified-random scheme. Commercial-type hydraulic clam dredges were modified to retain small individuals and used as survey gear; dredge specifications and vessels varied somewhat among cruises (Serchuk et al. footnote 10; Table 1).

We selected an area for intensive field study of ocean quahog growth, based on an evaluation of pre-1978 survey data and knowledge of commercial fleet activities. Specific criteria were: 1) sufficient clam densities for rapid capture of individuals used in the marking experiment, 2) abundant numbers of clams over a wide size range, 3) clam densities similar to sites frequented by fishing vessels, and 4) lack of previous exploitation and low probability of near-future use. These specifications were met at a site 48 km south-southeast of Shinnecock Inlet, Long Island, at lat. 40°25.1'N, long. 72°23.7'W. Water depth was 53 m, and substrata consisted of coarse sand and shell, primarily ocean quahog and sea scallop, *Placopecten magellanicus*. Live invertebrates present in survey samples included *Lunatia heros*, *Echinarachnius parma*, *Venericardia borealis*, *Aphrodite aculeata*, and *Astarte* spp., in addition to ocean quahog and sea scallop.

Water depth at the study site precluded extended periods of bottom time using normal scuba methods, thus we elected to sample ocean quahogs with commercial and research dredging vessels. The probability of recapturing marked ocean quahogs at the site was considered to be relatively low because of water depth, width of sampling gear, difficulties in positioning the vessel at a precise location, and the accuracy of the loran-C navigation system. Hence it was decided to mark and redistribute large numbers.

Incremental increases in clam shell growth corresponding to known time durations can be measured if a point of reference is initially established at the margin of the growing shell. Growth is determined directly from recaptured specimens and shell length at marking can either be measured or back-calculated. Thus we needed only to indelibly etch the shell edge of live quahogs and return them to the sea bed, obviating the laborious and time-consuming process of measuring and number-coding individuals prior to release.

Notching techniques have been used successfully to study growth rate and to validate the periodicity of band formation in a number of bivalve species including soft shell clam, *Mya arenaria* (Mead and Barnes 1904); hard shell clam, *Mercenaria mercenaria* (Belding 1912); American oyster, *Crassostrea virginica* (Loosanoff and Nomejko 1949); sea scallop (Stevenson

[10]Serchuk, F. M., S. A. Murawski, E. M. Henderson, and B. E. Brown. 1979. The population dynamics basis for management of offshore surf clam populations in the Middle Atlantic. Proceedings of the Northeast Clam Industries - Management for the Future, Coop. Ext. Serv. Univ. Mass.-MIT Sea Grant, p. 83-101.

TABLE 1.—Characteristics of survey gear and length-frequency statistics of ocean quahogs collected near lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight, 1970-80.

Vessel	Dates	Hydraulic dredge blade width (cm)	Spacing between[1] bars or rings (mm)	Shell length (mm)			
				$\bar{X}$	SD	Range	*n*
RV *Delaware II*	13 August 1970	122	30	[2]74.1	20.1	25-105	107
RV *Delaware II*	24 April 1976	122	30	74.1	16.6	40-115	271
RV *Delaware II*	27 February 1977	122	30	73.4	14.5	45-104	234
RV *Delaware II*	1 January-2 February 1978	122	30	74.5	14.3	34-113	211
FV *Diane Maria*[3]	26 July-5 August 1978	254	13	74.5	15.4	31-112	1,262
RV *Delaware II*	9 January 1979	152	25	71.4	14.5	33-116	1,317
RV *Delaware II*[4]	14-21 August 1979	152	25-51	76.5	15.2	38-111	811
RV *Delaware II*	8 February 1980	152	51	74.2	13.8	38-117	5,546
RV *Delaware II*[4]	9 September 1980	152	51	74.8	13.4	40-108	1,899

[1]Dimension in the portion of the dredge where catch is accumulated.
[2]Samples measured to the nearest 0.5 cm.
[3]Initiation of marking study.
[4]Recapture of marked individuals.

and Dickie 1954; Merrill et al. 1966); and surf clam (Ropes and Merrill 1970; Jones et al. 1978). Accordingly, we marked ocean quahogs by cutting shallow grooves from the ventral margin up the shell surface using thin carborundum discs mounted on an electric grinder (Ropes and Merrill 1970). Two parallel grooves 2 mm apart were cut into each shell to distinguish our marks from shells scratched by natural processes or during dredging (Fig. 1).

Marking operations were conducted from 26 July to 5 August 1978 (Table 1). A total of 41,816 ocean quahogs was notched by the previously described technique. Batches of 3,000-5,000 clams were dredged from within 9 km of the planting site, marked, and redistributed. The method of marking and planting clams was rapid; about 1,600 clams were marked per hour. A grid system based on loran-C coordinates, was used to indicate the location of each batch. Length-frequency samples were obtained during the marking phase (Table 1), and 134 small ocean quahogs (19-60 mm) were retained for maturity studies and analyses of exterior and cross-sectional banding.

An intensive effort to recapture marked individuals was undertaken, 1 calendar year after planting, during 14-21 August 1979 (Table 1). Forty-three hydraulic dredge tows, each of about 5-min duration, were completed at the site. A Northstar 6000[11] loran-C set and an Epsco loran-C plotter were used in the systematic search of a 20,000 m^2 area. A total of 14,043 ocean quahogs was examined; 74 (0.5%) had been marked. Recaptured specimens were photographed, measured, and frozen intact at sea. A random sample of 126 unmarked ocean quahogs was frozen for length-weight comparison with marked individuals.

Marked individuals were again recaptured, approximately 2 yr after planting, on 9 September 1980 (Table 1). Two dredge tows yielded 1,899 ocean quahogs; 249 individuals (13.1%) had been marked.

Length-frequency measurements were obtained from the site during routine assessment surveys in January 1979 and February 1980. Sampling within 10 km of the site was historically serendipitous; catch data were available from four surveys between 1970 and February 1978 (Table 1). Lengths of ocean quahogs taken near the site exhibited a consistent bimodal frequency distribution throughout the time-series. Growth rate information from the mark-recapture and shell banding experiments was thus compared with that generated from modal progression in sequential length frequencies.

A random sample of 278 ocean quahogs taken from the site during February 1980 was frozen whole for length-weight comparison with the August 1979 sample. Small ocean quahogs ($\leq$60 mm) were also frozen intact for analysis of the timing of periodic band formation in the shells.

LABORATORY STUDIES

Mark-Recapture

Recaptured specimens were thawed but kept moist during all phases of analysis to prevent shell cracking and disintegration of the periostracum. A total of 67 of the 74 specimens recaptured in 1979 and 200 of 249 specimens recaptured in 1980 were suitable for growth analysis; the remaining samples were either shell fragments or from quahogs obviously dead when recovered. Shells were measured to the nearest 0.01 mm, using calipers or dissecting microscope equipped with an ocular micrometer. Periostracum obscured the shell edge of most specimens and was subsequently removed from the vicinity of the mark prior to measurement. Shell lengths were obtained by pressing the periostracum against the valves with calipers.

Growth increments of recaptured ocean quahogs were determined as the linear increase in shell dimension along an imaginary line passing through the umbo and equidistant between grooves that formed the mark (Fig. 1). The linear distance between the umbo and shell edge at the mark was designed as h'; shell length at marking was computed for each quahog by:

$$SL_t = SL_{t+1} - \left[\frac{SL_{t+1}}{h'_{t+1}} \cdot (h'_{t+1} - h'_t) \right] \quad (1)$$

where SL_t = shell length (longest linear dimension) at marking,
SL_{t+1} = shell length at recapture,
h'_t = linear measurement between umbo and edge of the shell equidistance between grooves, at marking,
h'_{t+1} = linear measurement between umbo and edge of the shell

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

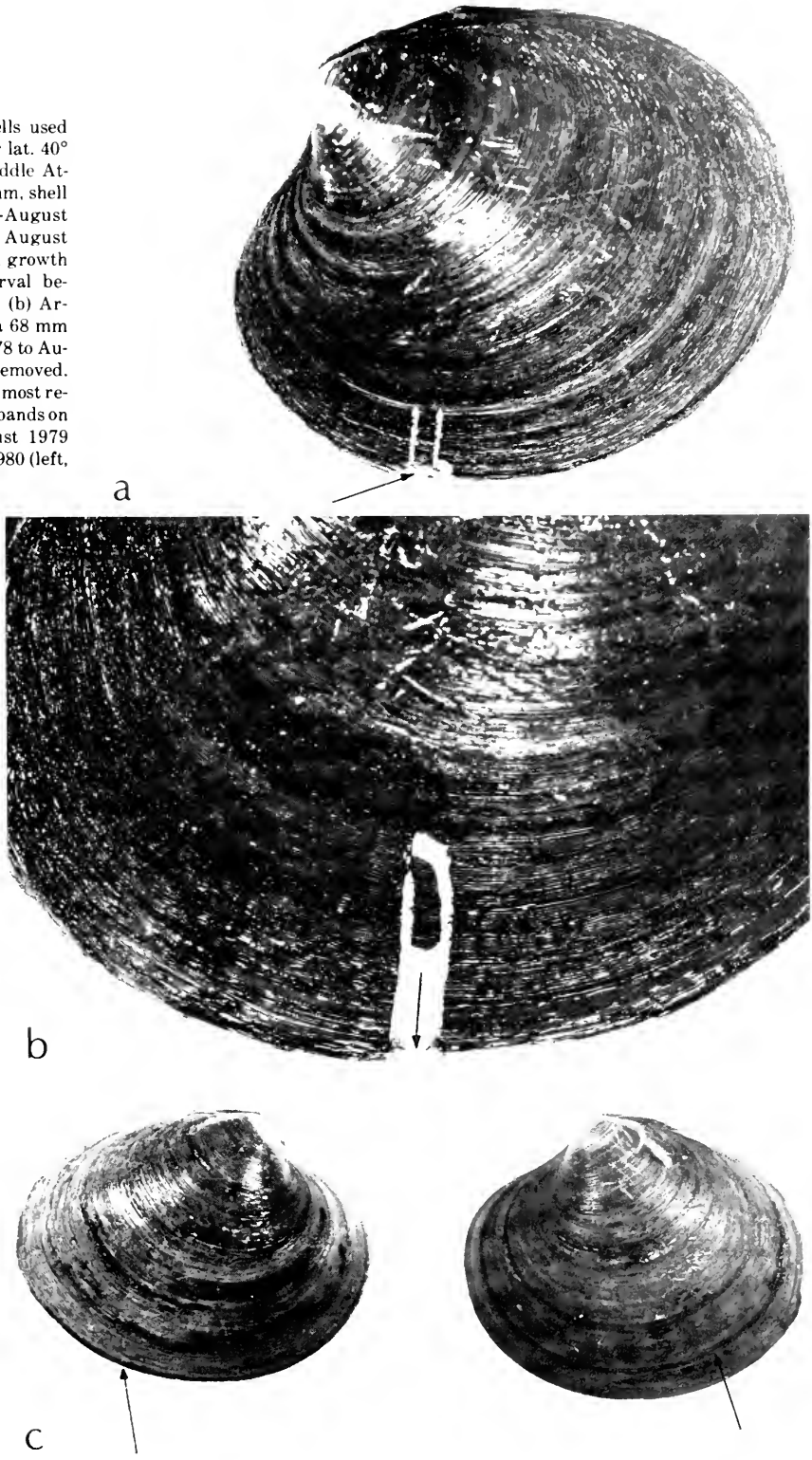

FIGURE 1.—Ocean quahog shells used for growth analyses taken near lat. 40° 25'N, long. 72°24'W, in the Middle Atlantic Bight. (a) Specimen 65 mm, shell length, marked during July-August 1978 and recaptured during August 1979. Arrow indicates external growth band formed during the interval between marking and recapture. (b) Arrow indicates shell growth of a 68 mm specimen from July-August 1978 to August 1979 with periostracum removed. (c) Arrows indicate positions of most recently formed external growth bands on small individuals from August 1979 (right, 43 mm) and February 1980 (left, 45 mm) samples.

equidistant between grooves, at recapture.

Marginal growth in shell length was thus equivalent to the bracketed term.

Implicit in Equation (1) is the assumption that ratios between the linear parameters SL and h' did not change between marking and recapture (isometric growth). The assumption is supported by comparisons of various standard shell dimensions (i.e., shell length, height, and width, Chandler footnote 6; Northeast Fisheries Center Woods Hole Laboratory unpubl. data), particularly considering the relatively small percent changes in shell size between marking and recapture (Table 2).

TABLE 2.—Growth of ocean quahogs marked during August 1978, and recaptured during August 1979 (n = 67), and September 1980 (n = 200), at lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight.

Parameter	Year	Mean (mm)	SD (mm)	Range (mm)
Shell length at recovery	1979	77.31	14.67	59.12-104.40
	1980	79.01	13.91	57.69-103.66
Calculated growth increment in shell length	1979	0.56	0.38	0.08-1.38
	1980	1.17	1.04	0.07-4.32
Calculated shell length at marking	1979	76.76	14.97	58.15-104.09
	1980	77.84	14.75	55.46-103.43

Three methods were used to fit growth equations to mark-recapture data. For ocean quahogs recovered 1 calendar year after marking, length at recapture was related to length at marking using Ford-Walford and linear annual increment plots described by Gulland (1969; Fig. 2). Additionally, a nonlinear exponential equation was fit to increment data and results compared with those assuming the von Bertalanffy model. The von Bertalanffy parameters L_∞ and K were also estimated using the BGC4 computer program (Abramson 1971). The program was designed for determining growth parameters when lengths of unaged individuals are known at two points in time, based on the algorithm of Fabens (1965).

Equations derived from mark-recapture data can be used to describe relative growth from an arbitrary point in time (i.e., SL_{t+1}, SL_{t+2}, ... SL_{t+n}), but without at least one independently derived age-length observation, absolute growth curves cannot be established. Accordingly, analyses of external banding patterns of small ocean quahogs were critical in "fixing" growth curves from mark-recapture.

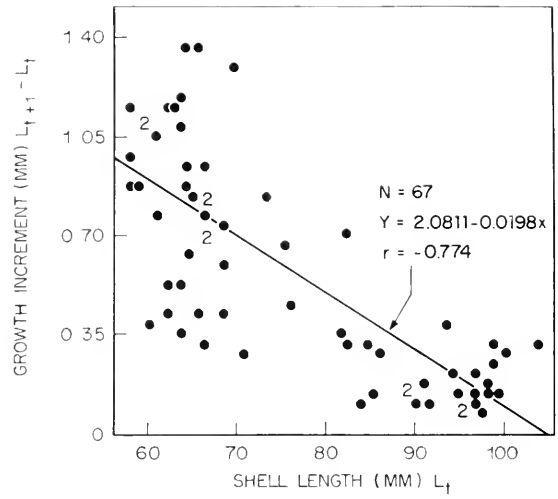

FIGURE 2.—Relation between calculated increment of growth in shell length (millimeters) and initial length for ocean quahogs marked during July-August 1978 and recaptured during August 1979 near lat. 40°25′N, long. 72°24′W, in the Middle Atlantic Bight.

Shell Banding

Small ocean quahogs retained from the July-August 1978 cruise were analyzed for external and internal shell banding patterns. Sequential growth of individual ocean quahogs was followed by measuring the maximum dimension (shell length) of exterior bands appearing on the periostracum, using calipers (Fig. 1). Maximum shell length beyond the last band was also recorded. The opposite valve was sectioned from the umbo to the ventral margin and polished (Saloman and Taylor 1969; Jones et al. 1978). An acetate impression of the polished surface was made and mounted between glass slides. Images were enlarged with a microprojector to reveal internal banding patterns.

Internal lines present in shell cross sections correlated in number and position with external bands when the latter were distinct. The periostracum on some shells was eroded near the umbo, obscuring external bands. In these cases "annuli" nearest the umbo were located on the peels, but measurements of shell size could not be made (Table 3). External marks present near the shell margins on some larger specimens also could not be discerned; internal banding was again used to estimate age. Shell length statistics were computed for each age/annulus subclass, weighted lengths at annuli for all ages and

TABLE 3.—Back-calculated growth (shell length, in millimeters) of small ocean quahogs. Samples taken from lat. 40°25′ N, long. 72°24′ W, 26-29 July 1978, in the Middle Atlantic Bight.

Number of annuli		Length at capture	Length at annulus												
			1	2	3	4	5	6	7	8	9	10	11	12	13
2	$\bar{x}$	18.00	7.00	12.30											
	SD	0.00	0.00	0.00											
	n	1	1	1											
3	$\bar{x}$	23.36	4.59	10.59	18.01										
	SD	3.42	0.78	2.66	3.14										
	n	9	9	9	9										
4	$\bar{x}$	29.73	4.39	10.04	16.99	24.38									
	SD	2.00	0.73	2.13	2.38	1.96									
	n	14	14	14	14	14									
5	$\bar{x}$	34.58	4.43	8.80	14.45	21.72	29.72								
	SD	3.19	0.07	1.50	2.29	3.08	3.41								
	n	26	26	26	26	26	26								
6	$\bar{x}$	38.49	4.07	7.77	13.40	19.13	26.09	33.88							
	SD	2.73	0.59	1.57	2.49	2.58	2.73	2.92							
	n	27	[1]25	27	27	27	27	27							
7	$\bar{x}$	41.66	4.16	7.66	12.10	17.42	23.87	30.81	37.61						
	SD	2.00	1.10	1.34	1.72	1.57	1.87	1.98	2.05						
	n	29	[1]27	29	29	29	29	29	29						
8	$\bar{x}$	46.24	3.92	7.59	12.29	16.92	23.64	29.95	36.63	42.76					
	SD	1.78	0.98	1.44	2.39	2.77	2.38	2.52	2.22	1.99					
	n	10	10	10	10	10	10	10	10	10					
9	$\bar{x}$	47.60	3.10	7.50	11.00	15.90	21.30	27.40	33.50	39.20	44.90				
	SD	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00				
	n	1	1	1	1	1	1	1	1	1	1				
10	$\bar{x}$	48.23	3.67	6.47	11.77	15.97	20.80	25.57	31.17	36.90	40.40	45.30			
	SD	0.59	0.29	0.50	1.19	2.48	2.31	2.35	1.89	2.07	0.36	0.30			
	n	3	3	3	3	3	3	3	3	3	3	3			
11	$\bar{x}$	54.35	3.90	5.70	9.35	13.80	20.30	27.60	34.20	40.20	44.45	48.50	51.95		
	SD	2.05	0.00	0.42	0.78	0.28	3.68	4.81	2.83	1.41	1.06	0.71	1.20		
	n	2	[1]1	2	2	2	2	2	2	2	2	2	2		
12	$\bar{x}$	53.87	3.73	7.23	10.07	12.97	19.13	27.00	31.60	35.67	39.50	43.50	44.75	49.55	
	SD	3.95	0.35	1.38	2.30	3.28	4.15	9.37	8.56	7.90	8.42	8.23	1.91	2.90	
	n	3	3	3	3	3	3	3	3	3	3	3	[2]2	2	
13	$\bar{x}$	53.90	—	5.20	9.70	12.80	17.50	22.20	28.00	34.70	38.30	43.70	46.40	50.00	52.00
	SD	0.00	—	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	n	1	[1] —	1	1	1	1	1	1	1	1	1	1	1	1
14[2]	$\bar{x}$	51.15	3.85	7.30	10.65	15.30	22.40	29.10	33.75	38.75	43.40	48.10			
	SD	5.16	0.50	2.26	2.19	0.42	0.57	1.56	1.34	0.07	1.98	0.00			
	n	2	2	2	2	2	2	2	2	2	2	1			
16[2]	$\bar{x}$	57.93	4.00	6.95	12.05	18.50	24.80	31.53	37.25	42.60	46.57	50.30	55.30		
	SD	2.90	0.00	1.11	2.24	2.49	3.95	3.75	2.91	2.60	1.59	1.84	0.00		
	n	4	[1]2	4	4	4	4	4	4	4	3	2	1		
18[2]	$\bar{x}$	57.10	3.60	7.55	10.95	16.40	24.60	29.85	40.10	43.40	46.80	49.00			
	SD	0.99	0.00	2.05	3.89	5.80	5.37	4.46	0.00	0.00	0.00	0.00			
	n	2	[1]1	2	2	2	2	2	1	1	1	1			
ALL	$\bar{x}$	38.94	4.21	8.27	13.59	19.17	25.44	31.13	36.28	40.40	42.82	46.52	49.18	49.70	52.00
	SD	8.65	0.85	1.95	3.03	3.69	3.95	3.75	3.47	4.01	4.41	4.32	4.58	2.07	0.00
	n	134	125	134	133	124	110	83	56	27	16	13	6	3	1
	Min	18.7	2.5	5.1	7.8	9.3	14.5	18.6	24.5	29.3	32.4	36.0	43.4	47.5	52.0
	Max	60.4	7.0	15.8	22.5	26.7	36.4	38.1	41.9	46.2	48.8	52.3	55.3	51.6	52.0

[1]External mark eroded but mark present in shell cross section.
[2]Number of annuli exceeds the number of lengths at annulus because marks could be distinguished in shell cross sections that were too closely spaced to discern on shell surfaces.

lengths at capture were also determined (Table 3).

Specimens recaptured in 1979 ranged in shell length from 59 to 104 mm, most had a deep brown or black periostracum. Several specimens did, however, exhibit the characteristic external banding pattern (Fig. 1), and were useful in validating the presumed annual periodicity of marks.

Marginal shell growth beyond the last external mark was strikingly different among small ocean quahogs from August 1979 and February 1980 samples. Mean lengths at capture for individual age classes from summer 1978 (particularly ages 1-9) were substantially greater than lengths at the last annulus, and were nearly equivalent to mean lengths at the last annulus for the next age class (Table 3). Ocean quahogs from winter 1980 invariably had formed or were forming an annulus at the shell margin (Fig. 1). A similar pattern was noted in shell cross sections.

Modified exponential and logistic growth equations were fitted to mean back-calculated lengths at age, from the July 1978 samples (Table 3), using the asymptotic regression and nonlinear least squares computer programs BMDO6R and BMDO7R, respectively (Dixon 1977; Fig.. 3). Few aged shells were as large as those recaptured (Tables 2, 3). Growth functions generated from aging data were thus extrapolated to the size range of recaptured specimens and results compared with annual growth increments predicted from mark-recapture (Figs. 2, 3). An age-size point necessary to initiate the mark-recapture growth function was computed from growth equations fitted to age-length data generated in shell banding experiments; the mark-recapture equation was then iterated to encompass most shell lengths present at the marking site (Figs. 4, 5).

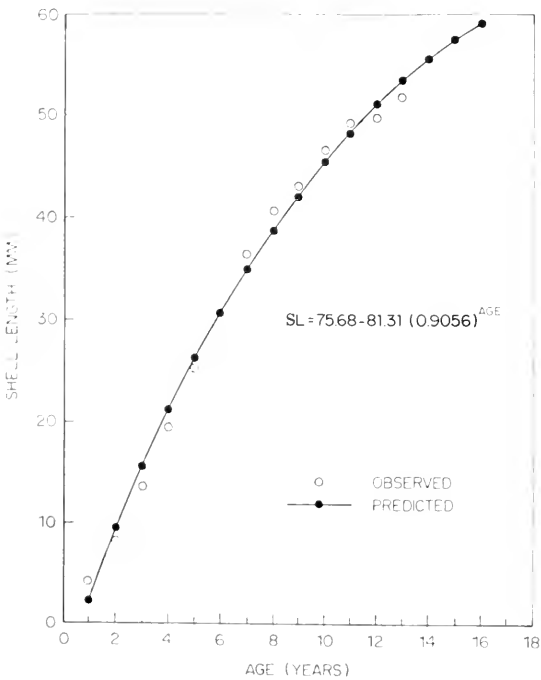

FIGURE 3.—Observed and predicted shell lengths at age for small ocean quahogs sampled during July 1978 near lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight.

Length-Weight

Shell length-drained meat weight relationships were computed for samples taken during August 1979 and February 1980. Laboratory

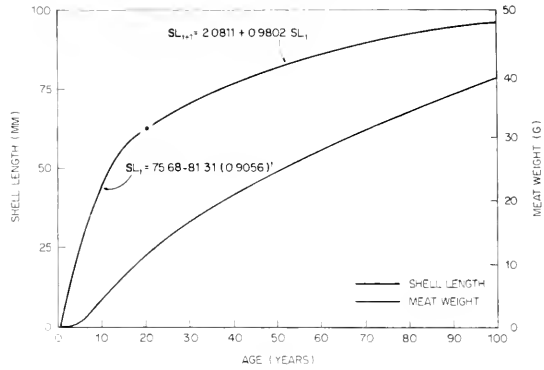

FIGURE 4.—Predicted shell lengths (millimeters) and drained meat weights (grams) at age for ocean quahogs at lat. 40°25′ N, long. 72°24′W, in the Middle Atlantic Bight. Growth in length is described by an equation derived from studies of external banding patterns of small individuals (left of dot), and the Ford-Walford equation from mark-recapture data (right of dot). Weights at age are derived by applying the overall length-weight equation presented in Table 5 to calculated mean lengths at age.

and statistical methods are given in Murawski and Serchuk (1979). Equations for recaptured and unmarked specimens from August 1979 were compared by covariance analysis to assess effects of marking (Table 4). Presumably, if physiological processes of the animal were significantly disrupted by the marking procedures, the adjusted mean of the length-weight equation might be statistically lower than that of controls. Seasonal variability in length-weight was investigated by comparing summer and winter equations (Table 5).

RESULTS AND DISCUSSION

New shell growth of recaptured individuals was clearly discernible in small specimens (<70 mm) not only at the mark, but all along the

TABLE 4.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for marked and unmarked individuals sampled at lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight, during August 1979.

	Linear regression parameters			
Sample	Intercept (*a*)	Slope (*b*)	*r*	*n*
Marked	−9.8373	2.9530	0.975	55
Unmarked	−9.0170	2.7637	0.953	126

	Test of adjusted mean			Test of slope	
Sample	Adjusted mean	df	*F*	df	*F*
Marked	2.8702	1,178	0.001 n.s.	1,177	2.13 n.s.
Unmarked	2.8714				

n.s. = $P>0.05$.

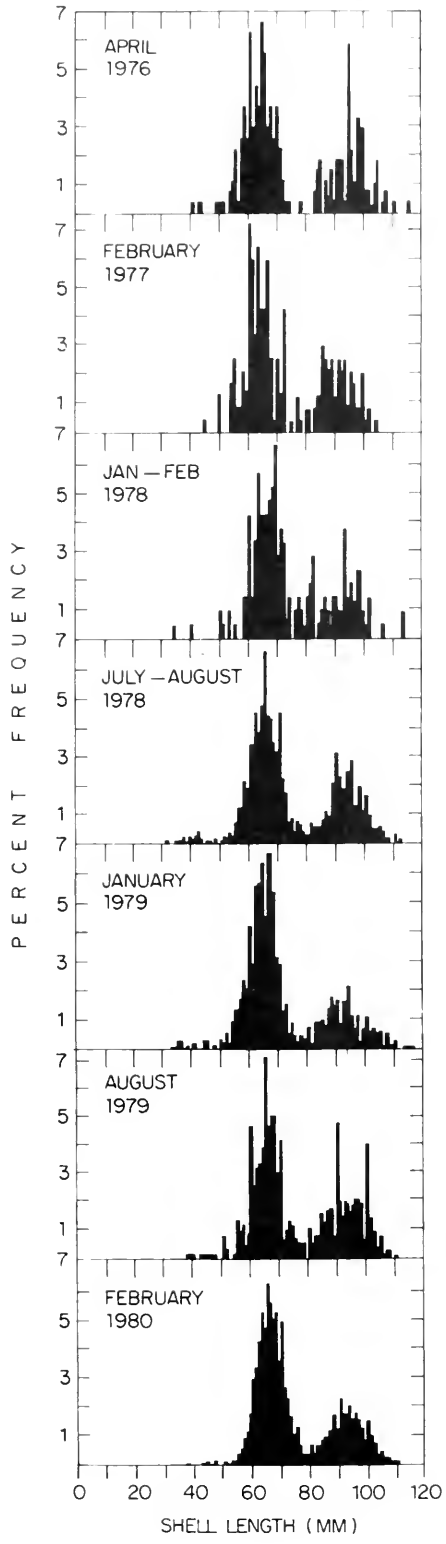

FIGURE 5.—Length-frequency distributions (1 mm intervals) of ocean quahogs sampled near lat. 40°25'N, long. 72°24'W, in the Middle Atlantic Bight, April 1976-February 1980.

TABLE 5.—Ocean quahog shell length-meat weight regression equations, and analysis of covariance for August 1979 and February 1980 samples taken near lat. 40°25′ N, long. 72°24′ W, in the Middle Atlantic Bight.

Sample	Linear regression parameters			
	Intercept (*a*)	Slope (*b*)	*r*	*n*
August 1979	−9.2901	2.8274	0.961	181
February 1980	−8.6865	2.7086	0.976	278
All data	−9.0627	2.7871	0.967	459

Sample	Test of adjusted mean			Test of slope	
	Adjusted mean	df	*F*	df	*F*
February 1980	3.0302	1,456	58.86**	1,455	3.22 n.s.
August 1979	2.9398				

**$P \leq 0.01$; n.s. = $P > 0.05$.

ventral margin when the periostracum was removed (Fig. 1). A growth interruption was produced at the previous shell edge of small specimens; new material was formed slightly below the earlier shell margin and was shinglelike in appearance (Fig. 1). Growth in larger ocean quahogs was less distinct and thus more difficult to measure. Where clear growth interruptions were not present, a faint yellowish band contrasting with white shell material was interpreted as a marking-induced check and growth was measured from that point. Shell growth was assessed midway between grooves that formed the mark since, in the case of larger specimens, the depth of the grooves was actually greater than the amount of new shell deposited (Figs. 1, 2).

A total of 11,658 ocean quahogs was measured directly from dredge catches at the marking site during 1970-80 (Table 1; Figs. 5, 6). Although minimum spacing of bars or rings in the rear portion of dredges varied somewhat (Table 1), size selectivity was apparently not significantly altered. Repeated tows were made at the marking site during August 1979 with 25 × 25 mm and later 51 × 51 mm wire mesh in the after portion of the dredge. Size distributions of ocean quahogs were nearly identical before and after the alteration. A possible explanation for the lack of differential selectivity is that shell, sand, and live invertebrates may have clogged the dredge at the beginning of tows, negating further filtering ability.

Two discrete length-frequency modes were exhibited in all sets of samples (Figs. 5, 6). Few small ocean quahogs (<50 mm) were encoun-

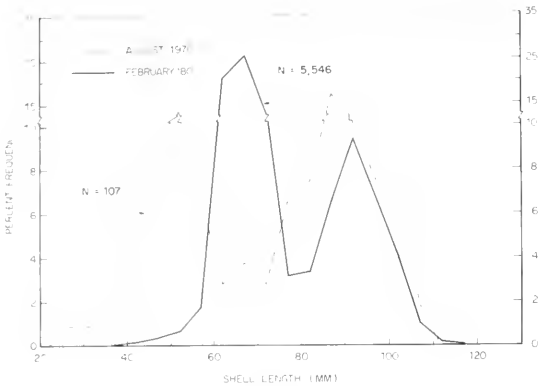

FIGURE 6.—Length-frequency distributions (5 mm intervals) of ocean quahogs sampled near lat. 40°25'N, long. 72°24'W, in the Middle Atlantic Bight, August 1970 and February 1980.

tered from 1976 to 1980 (Fig. 5) and, considering uniformity of modes over time, recruitment was probably equally poor during 1971-76. Thus, corresponding modes in the 1970 and 1980 samples were probably composed of the same year classes (Fig. 6). Average size of the small mode increased about 13 mm during the 9½-yr interval between August 1970 and February 1980, while the large group shifted about 3 mm (Figs. 5, 6; Table 1). Size progression of modes was minimal during 1976-80; intersample variation may be primarily related to differential sample sizes (Table 1). The effects of a sevenfold increase in sampling intensity can be seen by comparing August 1979 and February 1980 frequencies. Modes are smoothed in the latter sample, yet respective peaks are at precisely the same 1 mm intervals in both (65 and 90 mm). Average shell sizes ranged from 71 to 77 mm; however, trends in shell length among samples were not apparent (Table 1).

The average lengths of recaptured ocean quahogs (Table 2) were slightly greater than concurrent length-frequency samples (Table 1), although length extremes of the marked individuals were not as great. Recaptured ocean quahogs also exhibited the bimodal length-frequency distribution (Fig. 2), indicating recaptured specimens represented a relatively unbiased sample of marked individuals and the ocean quahog population in the immediate vicinity of the study area. Calculated increments of shell growth from ocean quahogs recaptured in 1979 ranged from 0.08 to 1.38 mm, and averaged 0.56 mm (Table 2). Those recaptured in 1980 grew an average of 1.17 mm (range 0.07-4.32 mm). Thus, incremental growth approximately doubled between summer 1979 and summer 1980, implying growth rates were similar during the 2 yr of the experiment and that marking procedures probably did not significantly disrupt growth patterns. Growth increments of ocean quahogs at liberty 1 yr generally declined with increasing shell length, although there was substantial variation about a linear fit (Fig. 2). The linear equation for predicting annual increment of growth from initial length is given in Figure 2; the Ford-Walford equation is: $SL_{t+1} = 2.0811 + 0.9802\ SL_t$, where SL is shell length (in millimeters) at age t. An exponential equation fitted to data in Figure 2 ($Y = 14.1216$ (exp $(-0.0459X)$)) explained about 8% more of the residual variance about the predicted line than did the linear equation. However, growth rates implied from length-frequency analyses were substantially greater than those from the exponential fit, and were similar to rates computed from the linear (von Bertalanffy) model. Thus, the latter model was considered more valid. Estimates of the asymptotic length (L_∞) and growth coefficient (K) from two fitting methods are:

	BGC4	*Annual increment*
L_∞ (mm)	107.06	104.95
K	0.0195	0.0200

Values of L_∞ from the two methods are >99.5% (BGC4) and 98.5% (annual increment) of the cumulative 1980 length-frequency distribution at the study site. Estimates of K are relatively low and characteristic of slow-growing, long-lived species (Beverton and Holt 1959).

Analyses of shell banding features present in small specimens indicate both external and internal marks are produced once during the biological year in these sizes. Several of the small recaptured ocean quahogs exhibited concentric external rings, and these specimens formed one such band during the interval between marking and recapture (Fig. 1a). Studies of small unmarked individuals retained from summer and winter sampling demonstrate that external and internal marks generally correspond in number and position. Internal marks were particularly useful in age determination when external marks were eroded near the umbo or closely spaced at the shell margin. Small ocean quahogs captured during the summer exhibited wide

marginal increments of shell growth from the last external and internal marks to the shell edge, whereas winter samples had recently formed annuli (Fig. 1c; Table 3). Thus, mark formation probably occurs during the last half of the calendar year. These observations are consistent with data presented by Jones (1980). In a study of the seasonality of incremental shell growth, he noted that internal growth bands in shell cross sections were formed from September to February. The formation of growth bands apparently overlaps the spawning period (Jones 1980); however, both events may be related to other physiological or environmental stimuli since specimens that were reproductively immature formed bands concurrently with mature ocean quahogs.

Back-calculated mean lengths at age varied considerably depending on the subset of data analyzed in Table 3. Mean lengths at age for all year classes (bottom rows in Table 3) were generally smaller than mean lengths at the last complete annulus (rightmost diagonal vector), and growth of recent age groups (2-8) appeared more rapid than for older ocean quahogs (Lee's phenomenon; see Ricker 1969). However, conclusions regarding the growth of older age groups (9-18) are tenuous due to the relatively small numbers of these ages sampled (87% of the samples were ≤8-yr-old).

Age analyses were limited to ocean quahogs that exhibited suitable contrast on the shell surface to discern external concentric rings. Thus, the oldest aged ocean quahogs (particularly ages 14-18) may represent the smallest, slowest growing individuals of their year classes; faster growing individuals may have reached sizes associated with color changes of the periostracum. Nevertheless, back-calculated mean lengths at age for 14- to 18-yr-old ocean quahogs did not tend to be progressively smaller than means for ages 9-13, perhaps indicating that size selectivity of older individuals was not a significant bias (Table 3).

The objectives of fitting statistical models to age-length data were to describe growth during the juvenile and early adult phases of life, and more importantly, to predict ages associated with the lengths of the smallest recaptured specimens (59-65 mm) thereby linking the age-length data and mark-recapture results into a continuous growth function. Recognizing the disparate nature of data subsets in Table 3, a series of exponential and logistic growth equations were fitted to: 1) weighted mean back-calculated lengths at age for all quahogs, 2) weighted mean lengths at age for ages 2-8, and 3) mean lengths at the last completed annuli (rightmost diagonal vector) for ages 2-10 and 2-13. For our purposes, the applicability of a particular model fit was judged not only by the total amount of variance between length and age explained by the equation, but by predicted annual growth increments in the 59-65 mm range. An appropriate model would fit as much of the age-sample data as possible and yield calculated annual growth increments consistent with those observed from recaptured specimens.

Exponential equations utilizing weighted mean back-calculated lengths for ages 2-8, and lengths at the last complete annulus for ages 2-13 yielded unacceptable fits by our criteria. The former equation was calculated with information from the linear portion of the growth curve, predicted lengths beyond age 8 were unrealistically high. The latter equation incorporated one negative growth increment (between ages 11 and 12) and thus the calculated asymptote was only 62.8 mm; predicted annual growth near the asymptote was considerably less than observed increments for that size (Fig. 2).

The logistic growth equation fitted to weighted mean lengths at age for all ocean quahogs ($SL = 52.09/1 + \exp(2.4722 - 0.4702(t))$) was superior to the respective exponential fit considering the residual sums of squares criterion. The reverse was true for the logistic equation describing mean lengths at the last annulus for ages 2-10 ($SL = 43.12/1 + \exp(2.9361 - 0.8069\ (t))$). However, asymptotic lengths were, for both logistic equations, well below the range of shell lengths considered in the mark-recapture experiments. Thus, extrapolation of logistic age-length relationships, necessary for initializing the Ford-Walford equation, was not feasible. On the contrary, the two exponential equations yielded reasonable asymptotic lengths and adequately described ocean quahog growth relative to that inferred from modal progressions in 1970 and 1980 length-frequency distributions (Fig. 6) and observed growth increments (Fig. 2).

Exponential growth equations computed from weighted mean lengths at age for all ocean quahogs and mean lengths at the last annulus for ages 2-10 were: $SL = 75.68\text{-}81.31\ (0.9056)^t$ and $SL = 72.70\text{-}75.22\ (0.8935)^t$, respectively. Mean lengths at age predicted from the two equations generally reflect differences among data sets

over the range of shell sizes used to fit the functions; however, estimated lengths at age converge near the sizes of the smallest recaptured specimens. Estimated lengths at age 20 were 64.49 and 64.29 mm, respectively. Corresponding growth increments from age 20-21 were 1.06 and 0.84 mm, well within the range of observed growth for those sizes (Fig. 2). If calculated lengths at age 20 are assumed to be the starting points for the Ford-Walford equation ($SL_{t+1} = 2.0811 + 0.9802\ SL_t$), the two acceptable exponential equations yield virtually identical growth curves when the Ford-Walford relationship is iterated. Additional growth analyses were conducted using the regression equation fitted to weighted mean back-calculated lengths for all ages because the maximum amount of information was used and the equation's behavior in the vicinity of marking data was consistent with empirical observations. However, further research on the growth patterns of small ocean quahogs is indicated in order to resolve differences between various data subsets in Table 3 and thus to define a more appropriate growth model for these sizes.

A composite growth curve incorporating the aged samples and mark-recapture data is given in Figure 4. The Ford-Walford equation was iterated to age 100 and a predicted shell length of 96.91 mm. Although ocean quahogs reach a size of at least 117 mm in the vicinity of the marking site (Table 1), ages substantially in excess of 100 are not necessarily implied because of the statistical variability in the marking data used to fit the predictor (Fig. 2). Annual growth in shell length is rapid during the first 20 yr of life, but declines significantly thereafter. Average yearly shell growth is 6.3% at age 10, 0.5% at age 50, and 0.2% at age 100.

Estimates of the von Bertalanffy parameter t_0 (age at zero length) were computed as −27.29 yr and −27.62 yr for the BGC4 and annual increment equations respectively, with $SL_{20} = 64.49$ mm (Gulland 1969, equation 3.5). Although predicted lengths at ages >20 are similar to those in Figure 4, a relatively poor fit to younger ages results from both von Bertalanffy equations.

The validity of using the age-length functions given in Figure 4 to describe ocean quahog growth at the marking site can be assessed by comparing predicted growth to that from modal progressions in length-frequency samples. Frequency distributions from 1976 to 1980 exhibit inter-sample variability in the position of major modes but no progressive shifts are discernible (Fig. 5). However, expected growth during the 5-yr period (Fig. 4) was smaller than could probably be identified, given the precision of length-frequency sampling (Table 1; Fig. 5). Length modes can be used to compute growth at the site between August 1970 and February 1980 (Fig. 6). Average growth of the smaller mode (52 mm in 1970) was about 13 mm, and the larger mode (87 mm in 1970) added about 3 mm shell length during the 9½-yr interval (Figs. 5, 6). Ocean quahogs 52 mm in length are about 12-yr-old and average 21-yr-old at 65 mm; the estimated age of 87 mm individuals is 60 yr and 90 mm quahogs average 70-yr-old (Figs. 3, 4). Thus, predicted growth during the period 1970-80 is strikingly similar to that inferred from length mode progressions, implying that age analyses and mark-recapture data adequately describe historical ocean quahog growth at the site.

The age-length relationships presented herein have been computed for shell sizes in excess of 95 mm and ages up to 100 yr. However, computed relationships for large sizes (>65 mm) are based on average growth rates from mark-recapture results and not from aging of individual specimens. It is likely, based on these analyses, that ocean quahogs do reach 100 yr in age; however, direct age determination of large individuals is contingent upon development and validation of suitable methodologies. Internal banding patterns present in shell cross sections were useful in aging small specimens since formation of the bands apparently occurs once annually. Seasonal shell formation patterns (Jones 1980) and age analyses of large individuals based on internal banding (Thompson et al. 1980; Jones 1980) are generally consistent with our data. Analysis of shell cross sections of large recaptured specimens may be useful in determining the periodicity of internal banding and the validity of the aging technique for large ocean quahogs; study of this material continues.

The regressions of shell length vs. drained meat weight for marked and unmarked ocean quahogs taken during August 1979 were not significantly different in slope or adjusted mean (Table 4). If in fact soft-tissue robustness is a valid index of relative condition, then marked individuals apparently suffered no lasting effects from the stress of dredging and handling. This observation is supported by the conclusions that incremental shell growth of marked specimens was similar to that computed from progressive

length frequencies of the population as a whole, and growth rates of marked individuals were nearly equal between 1978-79 and 1979-80.

Length-weight equations from February 1980 and August 1979 were parallel (Table 5); winter samples were apparently heavier in drained meat weight at a given shell length than summer samples. However, the magnitude of predicted differences in weight at length was small (4-11% for 65-115 mm ocean quahogs). Differences may be related to weight changes associated with sexual development, or merely a statistical artifact. Samples from winter and summer were combined to predict average weight for a given length during the year (Table 5). The resulting length-weight equation was applied to computed lengths at age to derive an age-weight relationship (Fig. 4). Initial weight gains are proportionally greater than concomitant length increases, but growth rates are nearly identical at the oldest predicted ages. Average annual increases in drained meat weight are 18.1% at age 10, 1.6% at age 50, and 0.2% at age 100 (Fig. 4).

Growth rates determined from the examination of concentric external banding patterns indicate small ocean quahogs may grow faster off Long Island than in the Northumberland Strait and in Passamaquoddy Bay (Caddy et al. footnote 7). However, data are insufficient to conclude that a latitudinal cline in ocean quahog growth exists. Factors influencing growth rates in a particular area are speculative; however, density dependence must be considered. Murawski and Serchuk (footnote 2) noted relative population stability and poor recruitment for ocean quahogs in the Middle Atlantic during 1965-77. Stable population size, poor recruitment, and slow growth are characteristic of populations under density dependent regulation. Investigation of ocean quahog growth rates at various densities may help to elucidate their interrelationship and indicate the population consequences of cropping high density areas.

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LARVAL DEVELOPMENT OF *CITHARICHTHYS CORNUTUS*, *C. GYMNORHINUS*, *C. SPILOPTERUS*, AND *ETROPUS CROSSOTUS* (BOTHIDAE), WITH NOTES ON LARVAL OCCURRENCE[1, 2]

JOHN W. TUCKER, JR.[3]

ABSTRACT

Developmental series of 4 of the 12 species of *Citharichthys* and *Etropus* known from the western North Atlantic and Gulf of Mexico are illustrated and described. The series consist of *C. cornutus* (preflexion to nearly transformed, 2.2-17.4 mm body length, BL), *C. gymnorhinus* (preflexion to late transformation, 4.4-12.9 mm BL), *C. spilopterus* (preflexion to juvenile, 3.7-25.4 mm BL), and *E. crossotus* (preflexion to nearly transformed, 4.6-10.8 mm BL).

Data from this study and that for 2 species previously described permit identification of larvae of 6 of the 12 species. For the species investigated, caudal fin formula (4-5-4-4) is the most reliable indicator for the group of genera *Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*. Number of elongate dorsal rays, degree of cephalic spination, and pigmentation are most useful for determining genus for known forms. Number of elongate dorsal rays, number of caudal vertebrae, pigmentation, morphology, and number of gill rakers are most useful for identification of *Citharichthys* and *Etropus* larvae that have been described.

Citharichthys cornutus larvae have no pectoral melanophore, little notochordal pigmentation, heavy lateral pigmentation, 3 elongate dorsal rays, and develop 6 left pelvic rays and 25-26 caudal vertebrae. Flexion is complete at 9-10 mm SL and transformation at about 18 mm SL. Larvae have been collected during all seasons. Caudal fin development in *C. cornutus* is typical of the four species described here. *Citharichthys gymnorhinus* larvae have no pectoral melanophore, little notochordal pigmentation, light lateral pigmentation except for a caudal band, 3 elongate dorsal rays, and develop only 5 left pelvic rays and 23-24 caudal vertebrae. Flexion is complete at 7-8 mm SL and transformation probably at about 18 mm SL. Larvae have been collected during all seasons. *Citharichthys spilopterus* larvae have no pectoral melanophore, little notochordal pigmentation, light lateral pigmentation, a blunt snout, a deep body, 2 elongate dorsal rays, and develop 6 left pelvic rays and 23-24 (rarely 25) caudal vertebrae. Flexion is complete at 7-8 mm SL and transformation at 9-11 mm SL. Larvae have been collected from September through April. *Etropus crossotus* larvae have a melanophore at the base of the pectoral fin, heavy notochordal pigmentation, heavy lateral pigmentation, 2 elongate dorsal rays, and develop 6 left pelvic rays and 25-26 (very rarely 24) caudal vertebrae. Flexion is complete at 9-10 mm SL and transformation at 10-12 mm SL. Larvae have been collected in May and August and probably occur from March to August.

Twelve species of the flatfish genera *Citharichthys* and *Etropus* (subfamily Paralichthyinae, family Bothidae) are recognized from the western North Atlantic (Table 1). Because of their small size at maturity, these fishes are presently used only by the pet food and fish meal industries (Topp and Hoff 1972). However, the abundance of larvae (Richardson and Joseph 1973; Smith et al. 1975; Dowd 1978) and adults (Dawson 1969; Topp and Hoff 1972; Christmas and Waller 1973) indicates that some species may represent significant components of estuarine and marine food webs.

Larvae in the *Citharichthys-Etropus* complex are difficult to distinguish and are often ignored or classified as "unidentified bothids" in species composition analyses (e.g., Fahay 1975). Of the 12 western North Atlantic species, only *C. arctifrons* and *E. microstomus* have been described in detail (Richardson and Joseph 1973). *Citharichthys cornutus*, *C. gymnorhinus*, *C. macrops*, and *E. rimosus* have been briefly described by Dowd (1978). Larvae of the remaining species have not been reported previously. Hsiao (1940) mis-

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takenly described *Bothus* sp. larvae as *E. crossotus*.

In this paper I present descriptions of larvae of *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, and *E. crossotus* and summarize data useful for identifying *Citharichthys* and *Etropus* larvae.

MATERIALS AND METHODS

Abbreviations

The following institutional abbreviations are used: CP&L = Carolina Power and Light Company, Raleigh, N.C.; GCRL = Gulf Coast Research Laboratory, Ocean Springs, Miss.; GMBL = Grice Marine Biological Laboratory, College of Charleston, S.C.; LSU = Louisiana State University, Baton Rouge; NCSU = North Carolina State University, Raleigh; NMFS = National Marine Fisheries Service, NOAA (four laboratories—Beaufort, Galveston, Panama City, and La Jolla); OSU = Oregon State University, Corvallis; RSMAS = Rosenstiel School of Marine and Atmospheric Science, University of Miami, Fla.; SCMRRI = South Carolina Marine Resources Research Institute, Charleston; Texas A&M = Texas A&M University, College Station; UNC = University of North Carolina, Institute of Marine Sciences, Morehead City; USNM = U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C.; VIMS = Virginia Institute of Marine Science, Gloucester Point.

Specimens

Larval and juvenile specimens used in this study were obtained from several sources. Forty-seven *C. cornutus* specimens from SCMRRI (MARMAP ichthyoplankton survey) collections in the South Atlantic Bight and five specimens from RSMAS collections from the Gulf of Mexico off western Florida were used for morphometrics, counts, and general development. Seven additional RSMAS specimens were used for counts. Other specimens from NMFS (Beaufort) collections in Onslow Bay, off North Carolina, were used for comparison. Twenty-eight *C. gymnorhinus* specimens from SCMRRI collections and 12 from RSMAS collections were used for morphometrics, counts, and general development. Other specimens from NMFS (Beaufort) collections were used for comparison. Fifty-five *C. spilopterus* specimens from NCSU and personal collections in the Cape Fear River estuary, one from a CP&L collection in the ocean just off Cape Fear, and three from Texas A&M collections in the Gulf of Mexico off Texas were used for morphometrics, counts, and general development. Other specimens from Texas A&M, NMFS (Beaufort, Galveston, and Panama City), and RSMAS collections were used for comparison and additional count data. Thirty *E. crossotus* specimens from LSU collections from the Gulf of Mexico off Louisiana and one from a NCSU collection were used for morphometrics, counts, and general development. Other specimens from Texas A&M collections were used for comparison.

Comparative larval material of other species was also examined. *Citharichthys* sp. A (probably *C. abbotti*) specimens came from Texas A&M; *Citharichthys arctifrons* specimens from NMFS (Beaufort), SCMRRI, and VIMS; a *Citharichthys* sp. B (probably *C. dinoceros*) specimen from RSMAS; and *Citharichthys* (*macrops*?) specimens from GCRL, RSMAS, and VIMS. Larvae of the eastern Pacific species *Citharichthys sordidus*, *C. stigmaeus*, and *C. xanthostigma* came from NMFS (La Jolla). Other specimens of Pacific *Citharichthys* spp. came from OSU; *Etropus microstomus* specimens from NMFS (Beaufort) and VIMS; *Etropus* sp. A (probably *E. rimosus*) specimens from CP&L, NMFS (Panama City), and RSMAS; *Cyclopsetta fimbriata* specimens from NMFS (Beaufort), RSMAS, SCMRRI, and Texas A&M; and *Syacium papillosum* specimens from RSMAS and Texas A&M.

Juvenile and adult specimens were examined to determine permanent characters. Specimens of *C. arctifrons*, *C. macrops*, *C. spilopterus*, *E. crossotus*, *E. intermedius* (cf. *E. crossotus*), *E. microstomus*, and *E. rimosus* came from USNM; *Citharichthys cornutus* and *C. gymnorhinus* specimens from GMBL; *Citharichthys macrops* specimens from UNC and a personal collection; and *Citharichthys spilopterus* and *E. crossotus* specimens from NCSU.

Description of caudal skeleton development was based on study of the entire developmental series of *C. cornutus* and comparison with the series of the three other species described. Calcified components of the caudal skeletons of nearly all the specimens could be seen following light staining with Alizarin Red S in 1% aqueous potassium hydroxide solution. Twenty cleared and stained (Taylor 1967) specimens were exam-

ined: *C. arctifrons*, (2) 40, 117 mm SL; *C. cornutus*, (1) 51.5 mm SL; *C. spilopterus*, (2) 41.6, ~100 mm SL; *C. macrops*, (2) 45.7, ~100 mm SL; *E. crossotus*, (1) 49.4 mm SL; *E. microstomus*, (12) ~30-100 mm SL. Radiographs of juveniles and adults also were studied: *C. arctifrons*, (1) 100 mm SL; *C. cornutus*, (16) 30-67 mm SL; *C. gymnorhinus*, (3) 23-37 mm SL; *C. macrops*, (75) 47-113 mm SL; *C. spilopterus*, (65) 23-109 mm SL; *E. crossotus*, (62) 29-92 mm SL; *E. intermedius* (cf. *E. crossotus*), (2) 80, 92 mm SL; *E. microstomus*, (1) 66 mm SL; *E. rimosus*, (1) 104 mm SL.

Counts

All larvae were lightly stained with Alizarin Red S in 1% aqueous potassium hydroxide solution for making counts and observing the sequence of ossification. Most specimens were fairly transparent and internal structures were visible without clearing. The following counts were taken from larvae and juveniles with a stereomicroscope: precaudal neural spines, caudal neural spines, hemal spines, precaudal centra, caudal centra (including urostyle), caudal fin rays supported by each hypural element, dorsal fin rays, anal fin rays, left and right pelvic fin rays, left and right preopercular spines, left and right frontal-sphenotic spines, and left and right upper (premaxillary) and lower (dentary) larval teeth.

Morphometrics

Measurements of various body parts of representative specimens were made on the left side with an ocular micrometer in a stereomicroscope. The only exceptions were standard and total lengths of the six longest *C. spilopterus* (19.4-25.4 mm SL), which were made with dividers and a millimeter scale. Measurements are defined as follows:

Body length (BL) = snout tip to notochord tip for preflexion and flexion larvae (notochord length, NL); snout tip to posterior margin of hypurals for postflexion larvae and juveniles (SL).

Upper jaw length = snout tip to posterior margin of maxillary.

Lower jaw length = anterior tip of dentary to posterior margin of articular just above the angular.

Snout length = horizontal distance from snout tip to anterior margin of left pigmented eye.

Eye diameter = horizontal diameter of left pigmented eye.

Head length (HL) = horizontal distance from snout tip to anterior margin of cleithrum at the body midline.

Snout to anus length = horizontal distance from snout tip through midline of body to vertical line through anus.

Total length = snout tip to posterior margin of finfold prior to caudal fin ray development, then to posterior tip of longest caudal ray.

Head depth = greatest vertical depth of head; in preflexion larvae, this is near or just behind the posterior half of the eye, but with development the greatest depth is progressively more posterior.

Body depth at pelvic fin = vertical distance from dorsal to ventral body margin at base of second pelvic ray.

Body depth at loop of gut = vertical distance from dorsal to ventral body margin at the deepest part of the gut (*C. cornutus* and *C. gymnorhinus* only).

Body depth at anus = vertical distance from dorsal to ventral body margin at anus.

Body depth at third hemal spine = vertical distance from dorsal to ventral body margin at third hemal spine.

Caudal peduncle depth = prior to dorsal and anal fin formation, the vertical distance from dorsal to ventral body margin at the shallowest part of the caudal peduncle; after dorsal and anal fin formation, at the posterior edge of dorsal and anal fins.

Developmental Terminology

Body length is a useful basis for linking characters of unidentified specimens with those in larval descriptions. However, body length may not be the most appropriate basis for comparing larvae of different species, especially bothids, which undergo notochord flexion and transformation at different sizes, usually within a narrow range for a single species but over a wide range for the family or even within a genus (e.g., *Citharichthys*). In this paper, both body length and stage of development are indicated for developmental events. Stage of development is defined by degree of notochord flexion or degree of transformation. Terminology is similar to that of

Moser et al. (1977) and Sumida et al. (1979), with slight modification because of the peculiarities of bothid development.

Preflexion stage = notochord is straight.
Early caudal formation = a substage of preflexion in which the notochord is still straight, but the caudal fin has begun to form.
Flexion stage = notochord is turning upward. There are three substages: Early flexion = notochord is slightly flexed; midflexion = notochord is S-shaped and flexed about 30°-60°; late flexion = notochord is turned up and is no longer S-shaped but is not yet in final position.
Postflexion stage = notochord is in final position, but transformation is not complete.
Transforming larvae = those in which dorsal migration of the right eye can be detected with low magnification. The period of transformation is divided into thirds, depending on the position of the right eye.
Juveniles = those specimens in which the right eye has reached its final position on the left side of the head and in which all fin rays have formed. Reported size ranges at transformation are based on available specimens and might not encompass the full possible size ranges. Environmental stimuli inducing transformation may be encountered at different sizes.

Terminology of components of the caudal skeleton follows Amaoka (1969), except as noted. The caudal fin formula was described by Gutherz (1971) as the number of caudal rays supported by each caudal element, dorsal to ventral.

Gutherz (1971) described certain cranial spines of *Cyclopsetta fimbriata* larvae as originating from the sphenotic bones. Futch and Hoff (1971) described similar spines of *Syacium papillosum* larvae as originating from the frontal bones. In the *Citharichthys* and *Etropus* larvae I have examined, similar spines are at the suture between frontal and sphenotic bones. The origin of these could not be determined with certainty, and therefore they are called "frontal-sphenotic" spines.

For the larvae described here, the first elongate dorsal ray is actually the second ray of that fin.

Larval Identification

Four developmental series were assembled, primarily on the basis of similar meristics, shape, and pigmentation. Transforming larvae and juveniles were identified first by the presence of known adult characters. Additional larval characters observed in those specimens were then used to aid in identification of the smaller specimens.

Because all transformed specimens were sinistral and the right eye of all transforming specimens was migrating, it was decided that the four larval series belonged to one or more of the flatfish families Bothidae, Scophthalmidae, or Cynoglossidae. Morphological characters exhibited in the larval series and shared by larvae of these three families are lateral compression, deep head, deep abdomen, and looped gut, and in early larvae a raised and rounded dorsal profile of the head and slender caudal region. Only one scophthalmid species, *Scophthalmus aquosus*, is known from the western North Atlantic (Gutherz 1967; Hensley 1977). The distinctive rhomboid shape, long-based pelvic fins, and dense pigmentation of *S. aquosus* larvae were lacking in my series of larvae. The small eyes, small head, and confluent dorsal, caudal, and anal fins of cynoglossids were also lacking. In addition, cynoglossids from this region have fewer caudal (usually 9-14) and pelvic (usually 4 left, 0 right) rays than the specimens in my series. Therefore, Scophthalmidae and Cynoglossidae were eliminated from consideration.

Gutherz (1971) summarized known characters most useful for identifying bothid larvae. Futch (1977) summarized subfamilial larval characters and tentatively recognized two subfamilies, Paralichthyinae and Bothinae. The following discussion is limited to western North Atlantic species. Four paralichthyine genera—*Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*—have a similar combination of transitory (larval) and permanent characters that distinguish them from other bothid genera. These include: 1) adult caudal fin ray formula of 4-5-4-4; 2) placement of the left pelvic fin on the ventral midline and the right above the ventral midline, both originating behind the cleithra (Gutherz 1971); 3) the same basic larval shape; 4) similar larval pigmentation—on the gas bladder, in dorsal and anal lines, and in the caudal region; 5) larval preopercular spines (at least in *Citharichthys cornutus*, *C. gymnorhinus*, *C. spilopterus*, *Cyclopsetta fimbriata*, *C. chittendeni*, *Etropus crossotus*, *E. microstomus*, and *Syacium papillosum*); 6) larval frontal-sphenotic spines (at least *Cith-*

arichthys arctifrons, *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, *Cyclopsetta fimbriata*, *C. chittendeni*, *E. crossotus*, *E. microstomus*, and *S. papillosum*). Caudal formula, pelvic fin placement, shape, and pigmentation of larvae in the four series corresponded to this group.

Cyclopsetta spp. have 26-28 caudal vertebrae (Gutherz 1967). Larvae of *C. fimbriata*, *C. chittendeni*, and *S. papillosum* have 5-10 elongate dorsal rays and well-developed preopercular and frontal-sphenotic spines (Gutherz 1971; Futch and Hoff 1971; Evseenko 1979). Futch and Hoff (1971) listed *Syacium* generic larval characters. Other *Cyclopsetta* and *Syacium* larvae are probably similar. Larvae in the four developmental series had lower caudal vertebral count ranges than *Cyclopsetta* spp., only 2-3 elongate dorsal rays, and relatively small preopercular and frontal-sphenotic spines. Therefore, these two genera were ruled out, leaving *Citharichthys* and *Etropus*. Identification to species is described in the individual species accounts.

For aid in determining species of *Citharichthys* and *Etropus*, frequency distributions of caudal vertebral, anal ray, and dorsal ray counts were tabulated from the literature, and from radiographs of juveniles and adults from the Atlantic off the southeastern United States (Append. Tables 1-3). Ranges of gill raker counts were tabulated from the literature (Append. Table 4). Number of caudal vertebrae (Append. Table 1) was the count most useful for distinguishing larvae. Vertebral counts can be made before ossification during early or midflexion, and overlap is not excessive. However, care is necessary to avoid inaccurate counts because of fused centra. Caudal neural spines and hemal spines, both of which number one less than caudal vertebrae, will stain with alizarin and sometimes can be counted before caudal vertebrae, during early or midflexion. The number of gill rakers on the lower limb of the first arch (Append. Table 4) can be counted in most specimens during transformation and can be very useful for identification of older larvae. The number of anal rays (Append. Table 2) is next in usefulness, followed by the number of dorsal rays (Append. Table 3); however, the overlaps for these counts are great. Efficiency can be gained by plotting individual anal versus dorsal counts on a graph, so that the counts can be used simultaneously. The adult complements of anal and dorsal rays are present by the end of transformation.

After the largest specimens in each series were identified, the identities of successively smaller larvae were verified. The most useful characters for untransformed specimens were lateral, pectoral, and notochordal pigment; number of elongate dorsal rays; number of caudal vertebrae; number and size of left pelvic rays; and head shape.

DESCRIPTION OF DEVELOPMENTAL STAGES

Citharichthys cornutus (Figs. 1-5)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (27)
Caudal vertebrae = 25(11)-26(16)
Gill rakers (lower limb, first left) = 12 (1)
Left pelvic rays = 6 (17)
Anal rays = 60-66 (11)
Dorsal rays = 78-84 (11)

Of the potential species listed in Table 1, only *C. cornutus* has counts that agree with these. In addition, larvae were captured over the outer shelf, slightly farther offshore than *C. gymnorhinus* (Fig. 1). This is consistent with bathymetric distribution of adults.

Distinguishing Characters

Citharichthys cornutus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Three elongate dorsal rays are present from preflexion (about 4 mm) through transformation. Caudal vertebrae (25-26) can be counted by early flexion (6 mm). Lateral pigment is relatively heavy. Flexion is complete at 9-10 mm SL. The larval mouth and eye are large. Morphology is similar to that of *C. gymnorhinus*. However, the left pelvic fin of *C. cornutus* has a full complement of six rays, and in larvae the first ray is not reduced in size. The left pelvic fin of *C. gymnorhinus* has only five rays, and in larvae the first ray is much reduced compared with that of *C. cornutus*. Length of *C.*

TABLE 1.—Distribution of adults of *Citharichthys* and *Etropus* species known from the western North Atlantic and status of knowledge of their larvae.[1]

Species	Geographic range of adults	Depth range of adults (m)	Larval descriptions
C. arctifrons	Georges Bank to Yucatan	22-682	Richardson and Joseph 1973
E. microstomus	New York to South Carolina	5-91	Richardson and Joseph 1973
C. cornutus	Georgia to Brazil	27-366	This paper
C. gymnorhinus	Florida to Guyana	37-201	This paper
C. spilopterus	New Jersey to Brazil (rare north of Virginia)	1-73	This paper
E. crossotus	Chesapeake Bay to French Guiana	1-86	This paper
C. macrops	Southern Atlantic and Gulf coasts of the United States	1-91	Brief description in Dowd 1978
E. rimosus	North Carolina to Mississippi River	5-190	Brief description in Dowd 1978
C. abbotti	Veracruz to Campeche, Mexico	0-2	Unknown
C. amblybregmatus	Western Caribbean off Nicaragua	139-197	Unknown
C. arenaceus	West Indies to Brazil	Shallow	Unknown
C. dinoceros	Florida to Nicaragua	183-1829	Unknown
C. uhleri[2]	Haiti		Unknown
E. intermedius[3]	Trinidad to Rio de Janeiro	27	Unknown

[1]Distributions compiled from Goode and Bean 1896; Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; Wenner et al. 1979; and original data for *C. spilopterus*, *E. crossotus*, and *C. macrops* (i.e., 1 m depths).
[2]cf. *C. arenaceus*, Dawson 1969.
[3]cf. *E. crossotus*, Gutherz 1967.

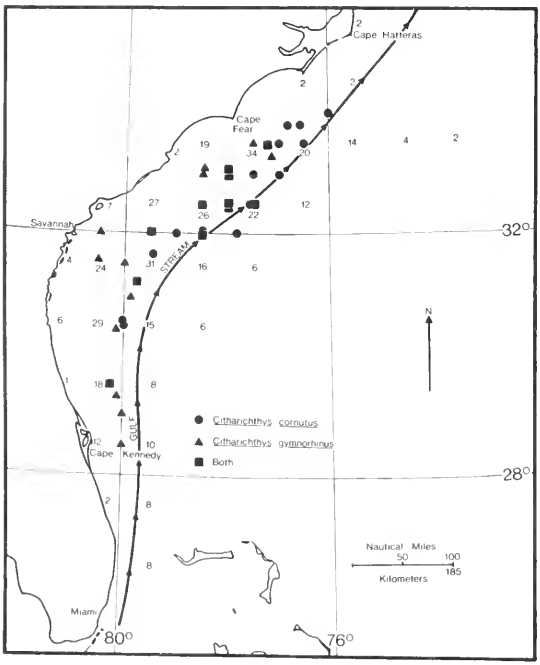


FIGURE 1.—Occurrence of *Citharichthys cornutus* and *C. gymnorhinus* larvae off the southeastern United States. Numbers are the sums of bongo and neuston tows made per 1° quadrangle during four RV *Dolphin* fall, winter, and spring cruises in 1973 and 1974. Symbols indicate positive tows.

cornutus at transformation is about 18 mm. Larvae may appear in collections year-round.

Pigmentation

Pigmentation of *C. cornutus* larvae is relatively heavy. Gas bladder, gut, and lateral tail pigment are the most striking. By 2.2 mm NL and throughout larval development, the dorsal one-third of the left side of the gas bladder is fairly heavily pigmented. This pigment may be diffuse or in the form of stellate or punctate melanophores. With growth, the number of melanophores increases. The maximum number in a preflexion specimen was five (4.8 mm). The right side of the gas bladder is usually unpigmented.

During preflexion (2.2 mm, see Fig. 4A), two or three melanophores are present on both the dorsal and the ventral body margins about halfway between the anus and the notochord tip. Another one or two melanophores are present between these two clusters near the lateral midline. Later in development, pigment in this area forms a band. One or two small melanophores may be present on the ventral finfold just posterior to the hindgut. Three or four melanophores are on the caudal finfold near the ventral body margin just anterior to the notochord tip. Two melanophores are on the ventral surface of the gut loop; additional melanophores appear there during development. A small melanophore appears along the posterodorsal surface of the midgut at about 3 mm. Melanophores begin appearing on the ventral body margin anterior to the cleithrum at about 3 mm. At about 4.7 mm, one or two melanophores appear along the posterior margin of the articular.

Flexion larvae (see Fig. 4B) usually have four or five melanophores on the dorsal one-third of the left side of the gas bladder. Midlateral caudal pigmentation consists of up to six dashlike melanophores. Additional, dashlike clusters of pigment appear along the dorsal and ventral body

margins between the anus and the caudal fin base.

During midflexion (6 mm, see Fig. 4B), internal pigment appears along the dorsal notch between the midbrain and hindbrain, and one or two round melanophores appear below the notch. Visible internal notochordal pigment is restricted to the vicinity of the external caudal band. The dorsal surfaces of one to three forming centra are darkened by about 6 mm. Several melanophores are present along the ventral body margin from just above the tip of the urohyal to just behind the cleithrum. Internal pigment appears between the hindgut and anal fin origin by midflexion.

By late flexion (8 mm, see Fig. 4C), both sides of the gas bladder are obscured by body musculature, and pigment appears diffuse. Notochordal pigment appears as fine dashes along the dorsal surfaces of three to six centra of caudal vertebrae 15-21. As many as 30 or more melanophores may be present along the ventral surface of the gut loop. Pigment along the posterodorsal surface of the midgut extends to the gas bladder and appears as a black lining over the gut. One or more melanophores appear on or just behind the posterodorsal margin of the preopercle. Melanophores have developed along the elongate second left pelvic ray and begin to develop along the elongate dorsal rays at 8-9 mm. Some larvae have small melanophores near the distal tips of rays at the middle of both dorsal and anal fins. By 8 mm, a group of melanophores has appeared along the middle of the caudal fin. The posterior margin of the articular is covered with a stellate melanophore.

By postflexion (9 mm), myoseptal pigment is present in the caudal band as well as adjacent to dorsal and ventral lines. Internal pigment along the brain surface looks diffuse. Pigment appears on the dorsal fin membrane adjacent to the first dorsal ray at about 11 mm. Body musculature tends to obscure dorsal notochordal pigment in larvae longer than 12 mm. Additional midlateral dashlike melanophores appear near the caudal fin base at 13-14 mm (see Fig. 5A). By about 14 mm, all five dorsal and four ventral pigment lines have formed, and myoseptal pigment is well developed. A small amount of pigment is present along the anteroventral edge of the maxillary by about 14 mm. Late transforming larvae have about three small internal melanophores near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (barely visible through the opercle); these probably develop by about 14 mm. Ventral pigment from the urohyal to the cleithrum persists until late transformation. By late transformation (see Fig. 5B), midlateral dashlike melanophores are present anterior to the caudal band.

Morphology (Figs. 4, 5; Tables 2, 3)

General morphological features include lateral compression, a deep head, a deep abdomen, and a looped gut. In early larvae the dorsal profile of the head is raised and rounded and the caudal region is slender. The eye is nearly spherical during early development but becomes ellipsoidal in transforming larvae. A ventral choroid fissure is visible from 3-4 mm NL until about the end of the postflexion stage. The nasal capsule is visible by about 3 mm NL. The gas bladder is prominent just above the foregut until the end of postflexion. It bulges slightly on the left side of the body and is not as obvious on the right. A loop forms in the gut by 2 mm NL. The liver occupies a large portion of the anteroventral region of the abdomen. Adult morphometrics given in the following discussion were derived from Topp and Hoff (1972).

The mouth is relatively large in larvae and adults. Larval upper jaw length/BL increases slightly from 10.3% (preflexion) to 11.0% (flexion) and then decreases to 9.8% (postflexion). Adult upper jaw length/BL is 12.8%, range 11.8-13.7%. Larval upper law length/HL decreases from 37% to 34%. Adult upper jaw length/HL is 45%. Larval lower jaw length/BL increases slightly from 13.3% (preflexion) to 13.9% (flexion) and then decreases slightly to 13.0% (postflexion). Larval lower jaw length/HL decreases slightly from 48% to 46% and is only slightly greater than that of *C. gymnorhinus*.

Larval snout length is moderate. Larval snout length/BL increases slightly from 6.2% (preflexion) to 7.1% (flexion) and then decreases slightly to 6.3% (postflexion). Adult snout length/BL is 5.5%, range 4.8-6.2%. Larval snout length/HL is constant at about 22-23%. Adult snout length/HL is 19.5%.

The larval eye is large, and the relative size of the adult eye is greater than that of any other western North Atlantic *Citharichthys* or *Etropus* species except *C. amblybregmatus*. Larval eye diameter/BL is constant at 9.8% during preflexion and flexion and then decreases to 8.5% (postflexion). Adult orbit length/BL is 10.0%, range

TABLE 2.—Measurements (mm) of larvae of *Citharichthys cornutus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, R = on the dorsal ridge.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at loop of gut	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
2.2		0.33	0.12	0.27	0.62	1.1		[1]0.76	[1]0.61	[1]0.61	[1]0.53	[1]0.26		Pref	S
3.2	0.35	0.41	0.21	0.31	1.0	1.7		1.2	[1]1.1	[1]1.0	[1]0.79	[1]0.36		Pref	S
3.7	0.40	0.47	0.25	0.37	1.1	1.9	3.8	1.2	[1]1.2	[1]1.2	[1]0.88	[1]0.47		Pref	S
4.0		0.56	0.28	0.44	1.1	1.9		1.4	[1]1.4	[1]1.5	[1]1.2	[1]0.64		Pref	S
4.1		0.59	0.27	0.43	1.2	2.1	4.2		[1]1.3			[1]0.57		Pref	S
4.5	0.47	0.57	0.27	0.43	1.2	1.8	4.6	1.4		[1]1.4	[1]1.1	[1]0.65		Pref	S
4.5	0.44	0.61	0.23	0.40	1.1	1.9	4.6	1.5	[1]1.4	[1]1.5	[1]1.2	[1]0.63		Pref	S
4.6	0.50	0.71	0.29	0.47	1.3	2.2	4.7	1.8	1.7		1.5	0.83		ECF	S
4.8	0.51	0.66	0.26	0.48	1.3	2.2	5.0	1.6	[1]1.6	[1]1.6	[1]1.4	[1]0.82		ECF	S
4.9			0.28	0.47	1.3	2.1	5.0		[1]1.6	[1]1.8	[1]1.5	[1]0.83		ECF	S
5.0	0.58	0.73	0.37	0.53	1.5	2.2		1.7	1.9					ECF	S
5.7	0.48	0.63	0.32	0.50	1.5	2.3	5.8		1.9	1.9	1.9	1.1		ECF	S
5.7	0.53	0.65	0.35	0.52	1.5	2.5		2.0	1.9	2.0		1.0		ECF	S
5.8	0.65	0.81	0.33	0.63	1.7	2.7		2.2	2.5	2.6	2.5	1.6	0.57	Mid	S
6.0	0.63	0.78	0.40	0.53	1.7	2.4		2.1	2.2	2.4	2.2	1.4		Early	S
6.1	0.69	0.86	0.37	0.63	1.8	3.1		2.4	2.7	3.0	2.6	1.8	0.61	Mid	S
6.3	0.66	0.84			1.8	2.6	7.4	2.4	2.5			1.7	0.59	Mid	S
6.3	0.75	0.96	0.46	0.65		3.0		2.5	2.8	3.1	2.7	1.8	0.64	Mid	S
6.4	0.70	0.92	0.41	0.63	1.8	2.9	7.5	2.5	2.8	3.0	2.7	1.8	0.64	Mid	1
6.4	0.70	0.89	0.44	0.63	1.8	3.0	7.2	2.4	2.6	2.8	2.5	1.6	0.54	Mid	S
6.4	0.77	0.90	0.55	0.63		3.0		2.5	2.8	3.1	2.7	1.9	0.65	Late	1
6.9	0.87	1.1	0.53	0.73	2.3	3.2	8.6	2.8	3.2	3.6	3.3	2.3	0.88	Late	1
7.2	0.76	0.96	0.46	0.74	2.2	3.2		2.8	3.0	3.4	3.1	2.1	0.84	Late	S
7.2	0.77	1.0	0.47	0.75	2.2	3.2	8.7	2.7	3.0	3.5	3.3	2.2	0.80	Late	S
7.6	0.90	1.2	0.60	0.77	2.5	3.6		3.2	3.7	4.2	4.0	3.0	1.0	Late	S
7.6	0.77	0.99	0.51	0.73	2.2	3.6	9.2		3.0	3.2	3.0	2.3	0.82	Late	S
7.6	0.83	1.0	0.50	0.77	2.3	3.3		2.8	3.2	3.6	3.3	2.3	0.88	Late	2
7.6	0.84	1.1	0.50		2.3	3.7	9.3	3.0	3.6	4.0	3.5	2.6	0.90	Late	S
7.7	0.90	1.1	0.65	0.73	2.4	3.4		3.2	3.5	3.7	3.5	2.6	0.94	Late	S
7.9	0.81	1.0	0.54	0.74	2.4	3.9	9.5		3.5	3.8	3.6	2.5	0.90	Late	1
8.2	0.91	1.2	0.64	0.81	2.6	3.6			3.7	4.1	4.0	3.0	1.1	Late	1
8.2	0.87	1.1	0.62	0.76	2.5	3.6		3.1	3.4	3.5	3.3	2.5	0.87	Late	1
8.3	0.97	1.3	0.71	0.81	2.7	4.1		3.5	4.0	4.8	4.3	3.0	1.1	Late	1
8.3	0.96	1.2	0.51	0.85	2.6		10.5		4.0	4.6	4.1	3.0	1.1	Late	S
8.4	0.90	1.1	0.61	0.80	2.7	4.2	10.2	3.4	3.8	4.4	3.9	2.8	0.94	Late	1
8.6	0.90	1.1	0.66	0.81	2.7	4.1	10.7	3.2	3.7	4.4	4.1	3.0	1.0	Late	2
8.8	0.95	1.2	0.61	0.80	2.6	3.7		3.2	3.8	3.9	3.9	2.9	1.0	Late	2
8.9	0.90	1.1	0.62	0.80	2.6	3.9		3.4	3.8	4.1	3.8	2.9	1.0	Late	2
10.4	1.1	1.4	0.74	0.93	3.2	4.6	12.9	4.0	4.6	5.3	5.1	4.0	1.4	Post	3
10.6	1.1	1.5	0.77	1.0	3.2	4.8	13.2	4.1	4.8	5.8	5.6	4.1	1.5	Post	3
10.6	1.2	1.5	0.73	0.94	3.2	4.6		3.9	4.6	5.3	5.1	4.1	1.4	Post	1
10.9	1.2	1.5	0.79	0.99	3.2	4.3		4.0	4.7	5.7	5.3	4.1	1.4	Post	3
11.5	1.2	1.6	0.74	1.1	3.4	4.9	14.1	4.0	4.6	5.5	5.3	4.1	1.4	Post	3
12.0	1.1	1.6	0.89	0.99	3.5	4.6	14.7	4.3	4.9	5.1	5.2	4.3	1.4	Post	3
12.1	1.3	1.6	0.73	1.1	3.6	5.0		4.6	5.1	6.1	6.0	4.9	1.6	Post	2
12.8	1.1	1.6	0.64	1.1	3.5	5.0		4.4	4.9	5.8	5.5	4.6	1.6	Post	3
12.9	1.2	1.6	0.73	1.0	3.5	5.1		4.8	5.2	6.1	5.9	4.8	1.6	Post	3
13.0	1.2	1.6	0.72	1.0	3.5	4.8	15.9	4.5	5.4	5.9	5.9	5.3	1.6	Post	3
13.8	1.2	1.7	0.70	1.2	3.7	5.2		5.4	5.9	6.7	6.5	5.5	1.8	Post	3
15.4	1.4	1.8	0.95	1.2	4.0	5.6	18.5	5.1	6.1	6.9	6.8	6.1	1.9	Post	3
17.4	1.6	2.2	1.2	1.2	4.8	5.6	21.2	5.7	6.6	7.5	7.6	7.2	2.2	Post	3
17.4	1.7	2.1	1.0	1.5	4.8	5.6		6.3	6.5		7.7	6.8	2.0	Post	R

[1]Measurement does not include dorsal or anal pterygiophores

9.2-11.1%. Larval eye diameter/HL decreases from 36% to 30% and is similar to that of *C. gymnorhinus*. Adult orbit length/HL is 35.5%.

The head is relatively large in larvae and moderate in adults. Larval head length/BL increases from 28% (preflexion) to 30% (flexion) and then decreases to 28% (postflexion). Postflexion head length/BL is similar to those of *C. arctifrons* and *C. gymnorhinus*. Adult head length/BL is 28%, range 27-30%. Larval head depth/BL increases from 34% (preflexion) to 39% (flexion) and then decreases slightly to 36% (postflexion).

Larval snout to anus length is relatively great until postflexion. Snout to anus length/BL is 46% during preflexion and flexion and then decreases greatly to 39% (postflexion).

The body is relatively deep in larvae and moderate in adults. Larval body depth at pelvic fin/

TABLE 3.—Body proportions of larvae and juveniles of three species of *Citharichthys* and one species of *Etropus*. Except for body length, values are in percentage of body length (BL) or of head length (HL) and are given as: mean ± standard deviation (range). (Values derived from Tables 2, 5, 6, 7.)

Measurement	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*
Body length (mm)				
Preflexion	4 6 (3.2-5.7)	4 6 (4 4-5.0)	3 7	4 6
Flexion	7.4 (5.8-8.9)	6 7 (5.3-7.7)	6.4 (5.7-6.8)	6.8 (4.9-9.5)
Postflexion	12 9 (10.4-17 4)	10.4 (7.9-12.9)	9.4 (8.3-10.6)	10 2 (9.3-10.8)
Early juvenile			10.0 (8 7-11 6)	
Midjuvenile			20.5 (14.3-25.4)	
Upper jaw length/BL				
Preflexion	10.3±1.0(8.4-11.6)	9 5±0.7(8 3-10.3)	9 9	7 0
Flexion	11 0±0 6(10.1-12.5)	9.3±0 4(8 3-10.0)	7.2±0.8(6.3-7 9)	7.2±0.7(5.9-8.4)
Postflexion	9.8±0.8(8.6-10 8)	9 3±0.7(8.1-11.3)	6.7±0.6(5 6-7 9)	7 1±0.5(6.4-7 8)
Early juvenile			7.3±0 4(6 1-8 1)	
Midjuvenile			9.0±0 4(8.4-9.7)	
Lower jaw length/BL				
Preflexion	13.3±1.3(11.0-15.3)	11 5±1 0(10.2-12.9)	12.1	9.6
Flexion	13.9±0.9(12.4-15.5)	12 7±0 6(11 6-13.6)	9.9±0.7(9 1-10.4)	9.6±1.0(8 5-12.3)
Postflexion	13.0±0.8(11.9-14.4)	12.7±0.6(11.6-14.2)	9.1±0.5(8.2-10 2)	9.8±0.5(9.2-10 6)
Early juvenile			10.3±0.5(8 9-11.5)	
Midjuvenile			13.1±0.4(12.5-13 8)	
Snout length/BL				
Preflexion	6.2±0.7(5.1-7 4)	5 2±1.1(3.7-6.7)	7.5	5.2
Flexion	7.1±0.8(5.7-8 6)	5.8±0 6(4.9-7.0)	7.6±0.8(6.8-8 1)	6.4±0.7(5 1-7.5)
Postflexion	6.3±0.8(5.0-7 4)	6.1±0.6(4 8-7.6)	6.4±0.6(5.6-7 4)	6.8±0.9(5.4-7.6)
Early juvenile			5.8±0.6(4 4-7.2)	
Midjuvenile			5.0±0.5(4.3-5.5)	
Eye diameter/BL				
Preflexion	9.8±0.7(8.8-11.0)	8.8±0 5(8.1-9 5)	9.7	7 4
Flexion	9.8±0.5(8.8-10.8)	8.9±0.8(6.9-10.0)	7.9±0.2(7.6-8.1)	6.9±0.4(6.1-7.7)
Postflexion	8.5±0.6(7.2-9.4)	8.8±0.5(7.9-9.8)	6.5±0.6(5.5-7.6)	6 3±0.3(6.1-6 9)
Early juvenile			6.8±0.5(5 9-7 7)	
Midjuvenile			7.0±0.6(6.5-8 2)	
Head length/BL				
Preflexion	27 6±2 2(23.8-31 2)	24 8±1 0(23.8-26.6)	28.0	23.4
Flexion	30.4±1.5(28.0-33.1)	27.9±1.9(25.0-31.1)	26.4±0.8(25.5-27.0)	26.4±1.3(24 2-28.7)
Postflexion	28.4±1.6(25.9-30.5)	28.6±1.7(26.8-33.8)	23.9±1.0(22.4-25.7)	26.4±1.5(24 4-28.8)
Early juvenile			25.4±0.8(23.9-27.1)	
Midjuvenile			25.0±0.7(24.2-26.2)	
Snout to anus length/BL				
Preflexion	45.8±4 7(39.4-54 1)	43.0±1 2(42.0-45.1)	40.0	39.1
Flexion	45.9±2.9(40.1-51.2)	44 2±2.0(40.2-46 6)	39 0±1.4(37.5-40.2)	44.2±2 0(39 8-48.0)
Postflexion	39.3±4 1(32.1-45.8)	39.7±2.9(34.6-46.2)	31.8±1 2(29 7-33.5)	38.8±3.2(33.5-42.2)
Early juvenile			31.0±1.3(28.8-34.0)	
Midjuvenile			31.6±1 2(29.8-34.3)	
Total length/BL				
Preflexion	102.3±0.7(101 6-103.5)	102.0±0.6(101.5-102 9)	102.2	101.5
Flexion	121.0±3.9(112.3-126.5)	116 0±12 6(102.0-126 2)	128.0	115 0±8.8(100.7-127.4)
Postflexion	123.0±1.4(120 6-124.9)	121.3±1.0(119.8-122 5)	123.1±1 2(121.4-125.0)	122.3±1.3(119 7-123.4)
Early juvenile			123.9±2.0(119.4-129 4)	
Midjuvenile			125.4±1 6(123.4-128.0)	
Head depth/BL				
Preflexion	34 5±2.3(31.4-38.8)	29 0±1 8(26.7-31.4)	36.6	28.6
Flexion	38.7±2.0(34 3-42.5)	33 3±2.3(28.3-36.2)	39 4±2.0(38.1-41.7)	33.8±1 6(30.7-36 4)
Postflexion	36.2±1.9(32.9-38.8)	33.3±1.6(31.0-36.3)	32.8±1.1(31.0-34.9)	33.1±1.6(31.5-35.8)
Early juvenile			32.0±1.1(29.8-34.9)	
Midjuvenile			31.0±1 0(29.6-33.0)	
Depth at pelvic fin/BL				
Preflexion	33.6±2 0(31 2-37 6)	29.8±2.6(27.0-33.5)	40.3	26.2
Flexion	43.6±2.9(37.1-49.1)	37.5±3 1(31.9-42.7)	46.7±0.9(45.9-47.7)	39.0±4.0(32.7-49.7)
Postflexion	41.3±2.4(37.4-45.8)	39.0±1.7(36.4-43.9)	39.0±1.1(36.9-40.8)	40.2±2.4(36 2-43.6)
Early juvenile			37.2±1.2(34.7-40.3)	
Midjuvenile			35 0±0.9(33.3-36.4)	
Depth at loop of gut/BL				
Preflexion	33.7±1.9(31.0-37.0)	29.2±2.9(25.5-33.9)		
Flexion	48.4±4.4(39 6-57.4)	39 1±4 3(32.7-45.0)		
Postflexion	48.0±3.6(42.6-54.7)	43.9±2.2(41.5-50.2)		
Depth at anus/BL				
Preflexion	28.4±3.6(23.8-33 7)	24 9±2.5(22.4-29 2)	38.7	21 4
Flexion	44.5±4.0(36.1-52.4)	36.9±4 4(30.3-44 2)	50.6±1.2(49.2-51.4)	37.8±5.6(29.3-45.7)
Postflexion	46.6±2.8(43.0-52.9)	42.2±1.7(39.7-47.0)	42.9±1.6(39.9-44.9)	43.1±3 5(36.3-46.2)
Early juvenile			39.5±1.4(35.9-43.3)	
Midjuvenile			38.7±0.7(37.2-39.7)	
Depth at third hemal spine/BL				
Preflexion	15.6±2.5(11.2-19.5)	14 2±2.3(11.9-18.2)	22.6	11.6
Flexion	31.4±3.9(22.8-39.8)	26.6±4.3(19.7-33.2)	40.8±2.9(38.7-44.0)	28.2±7.3(18.2-39.1)
Postflexion	38.6±1.9(35.6-41.8)	34 8±2.8(28.6-42.0)	38.0±1.4(35.3-39.8)	37.7±1 5(36.2-40.2)
Early juvenile			37.0±1.4(34.6-40.0)	
Midjuvenile			40.2±1.0(39.0-42.3)	

TABLE 3.—*Continued.*

Measurement	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*
Caudal peduncle depth/BL				
Flexion	11.4±1.4(8.4-13.8)	11.6±1.6(9.3-14.4)	14.4±1.6(13.1-16.2)	9.6±3.0(4.7-13.4)
Postflexion	12.7±0.6(11.6-13.8)	13.2±0.7(12.2-14.7)	13.5±0.5(12.7-14.3)	12.6±0.6(11.8-13.4)
Early juvenile			13.6±0.6(12.2-14.6)	
Midjuvenile			11.4±0.6(10.0-12.3)	
Upper jaw length/HL				
Preflexion	37.4±2.7(32.6-40.7)	38.3±2.0(34.9-40.9)	35.6	29.9
Flexion	36.0±1.8(33.2-39.1)	33.3±2.1(29.2-37.6)	27.2±2.4(24.7-29.4)	27.2±2.4(21.6-30.5)
Postflexion	34.4±1.6(31.6-36.6)	32.6±1.9(29.4-37.5)	28.1±2.2(24.0-33.8)	26.9±1.1(24.7-27.6)
Early juvenile			28.7±1.5(25.4-31.3)	
Midjuvenile			36.2±1.4(33.9-38.4)	
Lower jaw length/HL				
Preflexion	48.0±4.9(41.0-56.5)	46.5±3.2(42.7-51.2)	43.3	41.1
Flexion	45.5±2.9(39.5-51.4)	45.6±2.2(42.5-49.6)	37.5±1.4(35.9-38.6)	36.3±3.2(30.8-46.8)
Postflexion	45.9±1.1(43.6-47.7)	44.5±1.8(40.2-46.8)	38.2±1.7(35.9-41.5)	37.2±1.5(35.4-39.0)
Early juvenile			40.5±2.1(36.9-44.1)	
Midjuvenile			52.6±1.5(50.9-55.9)	
Snout length/HL				
Preflexion	22.4±1.5(20.2-25.2)	20.8±4.1(15.4-26.8)	26.9	22.4
Flexion	23.0±2.0(19.3-27.2)	20.9±1.6(19.0-24.6)	28.8±3.3(25.0-31.2)	24.3±1.9(21.0-28.0)
Postflexion	22.3±2.3(18.4-25.5)	21.3±1.9(17.6-24.0)	27.0±2.5(23.2-31.4)	25.9±2.7(22.3-29.1)
Early juvenile			23.0±2.3(18.3-27.1)	
Midjuvenile			19.9±1.7(17.5-22.5)	
Eye diameter/HL				
Preflexion	35.6±2.1(31.0-39.6)	35.4±2.2(32.3-38.2)	34.6	31.8
Flexion	32.2±2.1(29.6-37.5)	31.9±2.7(27.8-39.1)	29.9±0.5(29.4-30.3)	26.0±1.8(22.0-30.6)
Postflexion	29.9±1.5(26.3-31.7)	30.6±1.6(27.4-33.9)	27.1±2.0(23.4-31.1)	23.6±0.4(23.3-24.3)
Early juvenile			26.8±2.0(23.1-30.0)	
Midjuvenile			27.8±1.6(26.4-31.2)	

BL increases from 34% (preflexion) to 44% (flexion) and then decreases slightly to 41% (postflexion). Larval body depth at loop of gut/BL increases from 34% (preflexion) to 48% (flexion and postflexion). Larval body depth at anus/BL increases greatly from 28% to 47%. Larval body depth at third hemal spine/BL increases greatly from 16% to 39%. Adult body depth/BL is 46%, range 43-50%. Larval caudal peduncle depth/BL increases from 11.4% (flexion) to 12.7% (postflexion). Adult caudal peduncle depth/BL is 10.5%, range 9.7-11.4%.

Fin and Axial Skeleton Formation

Development of the caudal skeleton of *C. cornutus* from larva to juvenile (Fig. 2A-E) is typical of the four species described in this paper. The major difference among them is the rate of development. Flexion is complete at about 7-8 mm in *C. gymnorhinus* and *C. spilopterus* and at about 9-10 mm in *C. cornutus* and *E. crossotus*.

During preflexion, before caudal formation (2.2-4.5 mm NL), the notochord is straight and there is no evidence of hypural formation. During early caudal formation (4.6-5.7 mm NL, Fig. 2A) the notochord is straight and the outline of incipient hypurals 2+3 and 4+5 are visible, but neither hypurals nor incipient caudal rays are calcified.

During early flexion (6.0 mm NL, Fig. 2B) the notochord begins to turn upward. Hypurals 2+3 and 4+5 (sometimes hypural 1) and caudal rays begin to stain with alizarin, and the last neural and hemal spines stain with alizarin. Caudal rays form in about equal numbers dorsally and ventrally during flexion, beginning at the posteroventral corner of hypural 4+5 and the posterodorsal corner of hypural 2+3. The 6.0 mm specimen (Fig. 2B) was the smallest in which calcification of caudal rays had begun. During midflexion (6.1-6.4 mm NL, Fig. 2C) the notochord is S-shaped and hypurals 1 and 6 and the epural begin to stain with alizarin. During late flexion (6.4-8.9 mm NL, Fig. 2D) the notochord tip points upward and is nearly flexed but is still in contact with hypural 6 and the epural; all hypurals stain with alizarin and the last neural spine touches hypural 6. All rays are formed by about 7.5 mm NL.

When flexion is complete (10.4-17.4 mm SL, Fig. 2E) the urostyle is separate from hypural 6 and the epural, and all caudal rays stain with alizarin. Fusion of the epural with hypural 6, and fusion of hypural 4+5 with the urostyle occur at about the time of transformation. The terminology of Amaoka (1969) is followed here; however, actual fusion of hypurals 2 with 3 and 4 with 5 was not observed.

The adult caudal skeleton of *C. cornutus* (Fig. 3A) is composed of a urostyle, or terminal half

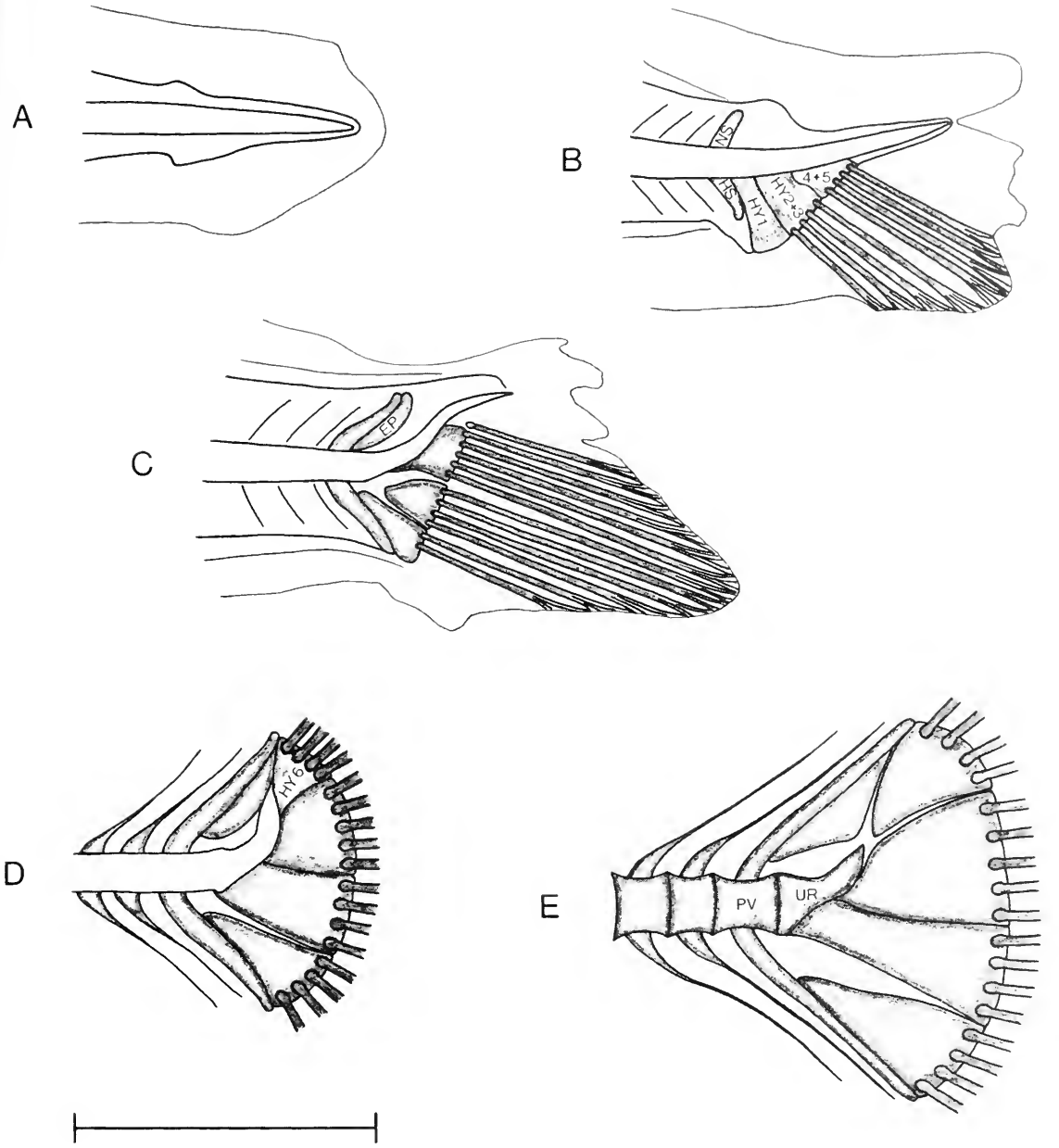


FIGURE 2.—Development of the caudal skeleton of *Citharichthys cornutus*: A. Preflexion (early caudal formation), 5.7 mm NL; B. Early flexion, 6.0 mm NL; C. Midflexion, 6.4 mm NL; D. Late flexion, 8.2 mm NL; E. Postflexion, 13.7 mm SL. NS = neural spine, HS = hemal spine, HY1 = hypural 1, HY2+3 = hypurals 2 and 3, 4+5 = hypurals 4 and 5, HY6 = hypural 6, EP = epural, PV = penultimate centrum, UR = urostyle. Scale = 1 mm.

centrum (according to Hensley 1977, in the bothid *Engyophrys senta* this bone consists of the first and second ural centra and the first preural centrum); a penultimate, or second preural, centrum (see Hensley 1977); an enlarged hemal spine from the second preural centrum supporting hypural 1; autogenous, proximally free, hypural 1 which supports three unbranched and one branched ray (equivalent to "parhypural" of some authors—e.g., Futch 1977; Hensley 1977—

see Sumida et al. 1979); autogenous, fused hypurals 2 and 3, articulating ventrally with the urostyle and supporting four branched rays; fused hypurals 4 and 5, fused with the tip of the urostyle and supporting five branched rays; an autogenous, proximally free element consisting of hypural 6 fused anteriorly with the single epural, one branched and three unbranched rays supported by hypural 6; no evidence of a uroneural; an enlarged neural spine from the second preural centrum supporting the epural. The caudal skeletons of the four species described here are similar to Amaoka's (1969) type 4, except for the lack of a uroneural.

Dendritic splitting of hypurals 2+3 and 4+5 occurs in *Etropus crossotus* by about 40 mm SL (Fig. 3B). The hypurals of adult specimens of *Citharichthys* spp. examined were sometimes grooved but never split as in *E. crossotus*. Hypurals 2+3 and 4+5 of *E. microstomus* and *E. rimosus* were similar to those of *Citharichthys* spp. except for an apparent tendency to split slightly at the distal margins.

In *C. cornutus* larvae all precaudal neural spines stain with alizarin by about 4.8 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.8 mm NL and all do by 6.1 mm NL. The urostyle stains with alizarin at 6.3 mm NL. All precaudal and caudal centra stain with alizarin by 7.2 mm NL. The smallest speci-

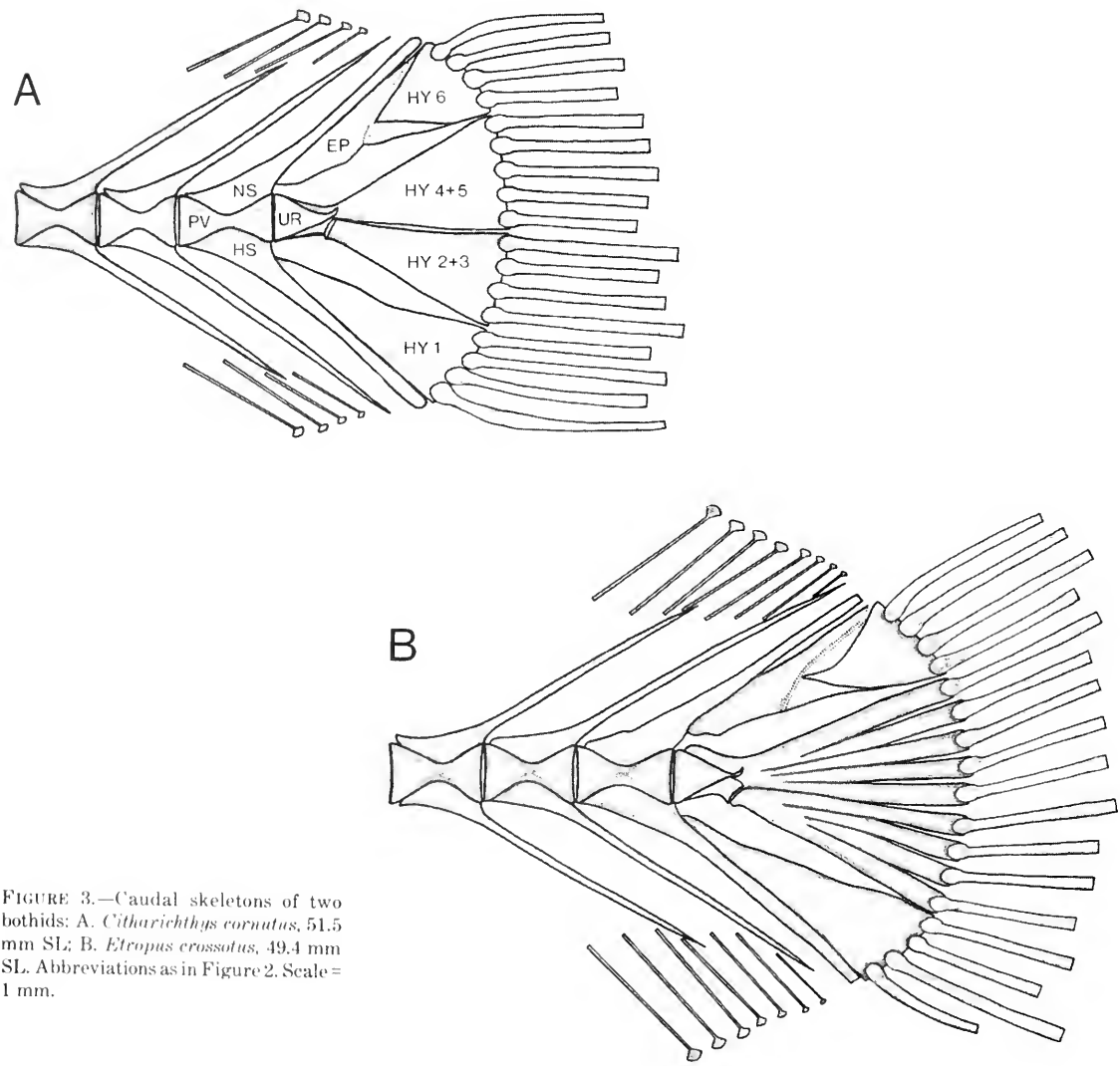


FIGURE 3.—Caudal skeletons of two bothids: A. *Citharichthys cornutus*, 51.5 mm SL; B. *Etropus crossotus*, 49.4 mm SL. Abbreviations as in Figure 2. Scale = 1 mm.

men in which caudal centra could be counted was 5.8 mm NL (midflexion).

The second, third, and fourth dorsal rays are elongate and widely separated at the bases from preflexion (about 4 mm NL) through transformation (17.4 mm SL). During early caudal formation (5.0 mm NL), rays near the middle of the dorsal fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (6.4 mm NL) onward. The first ray and the most posterior rays are calcified just prior to transformation (17.4 mm SL).

During early caudal formation (5.0 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8 mm NL) onward. The most posterior rays are calcified just prior to transformation (17.4 mm SL).

Development of the left pelvic fin precedes that of the right fin. The left pelvic fin bud appears during preflexion (3.7 mm NL). Rays develop between preflexion (4.0 mm NL) and late flexion (about 8.9 mm NL). The most anterior two rays are the first to appear; the second is elongate and the first slightly elongate. The right pelvic fin bud appears during early caudal formation (4.9 mm NL). Rays develop between midflexion (6.0 mm NL) and late or postflexion (9-10 mm BL). Each complete fin has six rays.

Rayless, fanlike, larval pectoral fins were present on the smallest available specimen (preflexion, 2.2 mm NL). Calcification of rays in the left fin occurs between about 13 mm and 17.4 mm SL. Calcification of rays in the right fin had not begun in the largest specimen (17.4 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (2.2 mm NL, Fig. 4A). With development (Fig. 4B, C), additional spines appear until maximum numbers of about 33 on the left (range 26-52) and 39 on the right (range 23-50) are reached during late flexion (6.4-8.9 mm NL). Thereafter, spines are lost until none or only a few remain at transformation (17.4 mm SL, Fig. 5B).

Frontal-sphenotic spines were evident in the second smallest preflexion specimen (3.2 mm NL) and throughout the larval series, though less conspicuous near transformation (13-17 mm SL). The lowermost spine on the left side is usually just above the center of the eye and on the right side slightly anterior to the center of the eye. (During transformation those on the right side are at the anterior margin of the skull.) The spines are arranged in a slightly posteriorly concave arch following the curve of the skull. There are usually six (up to eight) spines per side, including three stronger spines arising from a small bulge of the skull.

Larval Teeth (Table 5)

No teeth are present at 2.2 mm NL (Fig. 4A). At 3.2-4.1 mm NL, larvae usually have two upper and two lower teeth on each side. A 5.3 mm NL preflexion specimen had three upper and four lower teeth on each side. The same numbers were present in the largest early caudal formation specimen (5.7 mm NL). During flexion, numbers of teeth increase from about four upper and five lower (about 6 mm NL) to about eight upper and seven lower (8.9 mm NL) on each side. Postflexion larvae (10.4-13.8 mm SL) have about nine upper and nine lower teeth on each side. The nearly transformed specimen (17.4 mm SL, Fig. 5B) had fewer upper teeth on the left side (about 11) than on the right side (19) but the same number (about 15) in both lower jaws.

Transformation

Migration of the right eye may begin as early as midflexion (6.4 mm NL) or as late as postflexion (10.6 mm SL). The right eye moves from the right side of the head through a space between the dorsal fin and supraorbital bars (Fig. 5A) as in *Cyclopsetta fimbriata* (Gutherz 1971). The right eye reaches its final position on the left side of the head by about 18 mm SL. No early juvenile specimen was available, but eye migration in one of the 17.4 mm specimens was nearly complete (Fig. 5B).

Occurrence

Larvae were collected in the Atlantic during February, March, April, May, October, and November (Powles[4]). There was no apparent size progression by month, indicating an extended spawning season. Water depth was 46-640 m.

[4]H. W. Powles, Assistant Marine Scientist, South Carolina Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412, pers. commun. July 1976.

TABLE 4.—Number of left and right preopercular spines by stage of larval development. Pref = preflexion, ECF = early caudal formation (preflexion), Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion, Trans = right eye on or past dorsal ridge.

Species	Stage	BL range (mm)	Left			Right		
			$\bar{X}$	N	Range	$\bar{X}$	N	Range
Citharichthys cornutus	Pref	2.2- 5.0	12.1	7	4-18	12.7	7	4-19
	ECF	4.7- 5.7	18.2	4	13-20	19.8	4	18-23
	Early	6.0	23	1		22	1	
	Mid	5.6- 6.4	26.4	7	21-30	31.1	7	26-34
	Late	6.4- 8.9	32.9	19	26-52	38.7	19	23-50
	Post	10.4-13.8	22.0	8	11-33	33.8	8	24-44
	Trans	17.4	~0	1		~4	1	
Citharichthys spilopterus	ECF	3.7	31	1		27	1	
	Late	5.7- 6.7	31	2	26-36	35.5	2	33-38
	Post	8.3-10.2	16.0	7	2-29	20.0	6	11-32
	Trans	8.7-10.2	17.4	5	0-41	21.5	4	1-44
Citharichthys gymnorhinus	Pref	4.5- 5.4	15.3	3	13-17	17.0	3	16-19
	ECF	4.6- 5.3	20.0	2	19-21	14.0	2	11-17
	Early	5.3- 6.0	21.7	3	17-27	24.3	3	21-28
	Mid	6.6	21.0	2	19-23	27.0	2	26-28
	Late	6.7- 7.5	23.0	6	17-29	26.8	6	20-35
	Post	8.3-10.2	31.4	5	25-38	38.6	5	34-43
Etropus crossotus	ECF	4.6	17	1		19	1	
	Early	4.9- 5.4	19.0	2	17-21	21.5	2	21-22
	Mid	5.4- 6.0	24.5	10	18-29	22.0	10	16-27
	Late	6.1- 9.5	15.9	12	7-20	15.2	12	10-20
	Post	9.3-10.8	10.6	5	4-18	8.6	5	3-13
	Trans	10.3	0	1		2	1	

TABLE 5.—Number of larval teeth by developmental stage. Pref = preflexion, ECF = early caudal formation (preflexion), Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion, Trans = right eye on or past dorsal ridge, UJ = upper jaw, LJ = lower jaw.

Species	Stage and BL range (mm)	Jaw	Left			Right		
			$\bar{X}$	N	Range	$\bar{X}$	N	Range
Citharichthys cornutus	Pref	UJ	1.9	8	0- 3	1.9	8	0- 3
	2.2- 5.3	LJ	2.4	8	0- 4	2.4	7	0- 4
	ECF	UJ	3	3	3	3	5	3
	4.7- 5.7	LJ	3.5	4	3- 4	3.5	4	3- 4
	Early	UJ	4	1		4	1	
	6.0	LJ						
	Mid	UJ	5.8	4	5- 6	5.5	6	5- 6
	6.1- 6.4	LJ	6.5	4	6- 7	6.0	5	5- 7
	Late	UJ	6.6	20	5- 8	6.8	17	5- 8
	6.4- 8.9	LJ	6.8	13	6- 8	6.9	13	6- 8
	Post	UJ	8.6	10	8-10	8.9	8	8-10
	10.4-13.8	LJ	8.7	7	8-11	8.7	7	8-10
	Trans	UJ	~11	1		19	1	
	17.4	LJ	~15	1		~15	1	
Citharichthys spilopterus	ECF		2	1		2	1	
	3.7		3	1		3	1	
	Late	UJ	4	3	3- 5	4.3	3	4- 5
	5.7- 6.8	LJ	5	1		4.5	2	4- 5
	Post	UJ	4.0	6	3- 5	3.8	5	3- 4
	9.0-10.6	LJ	4.8	4	4- 5	5	1	
	Trans	UJ	4.8	5	4- 6	4	1	
	9.1-10.7	LJ	5.3	3	5- 6			
Citharichthys gymnorhinus	Pref	UJ	2.3	3	2- 3	2.3	3	2-3
	4.5- 5.4	LJ	2.7	3	2- 4	2.7	3	2-4
	ECF	UJ	2.5	2	2- 3	2.5	2	2-3
	4.6- 5.3	LJ	3.5	2	3- 4	3.5	2	3-4
	Early	UJ	3.3	3	2- 4	3.3	3	2-4
	5.3- 6.0	LJ	4.5	2	4- 5	4.5	2	4-5
	Mid	UJ	4.7	3	4- 5	4.5	2	4-5
	6.4- 6.6	LJ	5.5	2	5- 6	6	1	
	Late	UJ	5.7	6	4- 7	5.3	6	4-7
	6.7- 7.7	LJ	6.5	4	6- 8	6.5	4	6-8
	Post	UJ	7.1	11	6- 8	6.9	9	6-8
	7.9-12.9	LJ	8.0	7	6- 9	8.0	5	8
Etropus crossotus	ECF	UJ	3	1		3	1	
	4.6	LJ	5	1		5	1	
	Early	UJ	3	2	3	3	2	3
	4.9- 5.4	LJ	5.5	2	5- 6	5.5	2	5-6
	Mid	UJ	3.4	10	3- 5	3.4	10	3-5
	5.4- 6.0	LJ	6.4	8	5- 7	6.7	9	5-7
	Late	UJ	4.1	11	3- 5	3.8	9	3-4
	6.1- 9.5	LJ	7.0	10	6- 8	7	7	7
	Post	UJ	4.5	4	4- 5	5.2	5	4-7
	9.3-10.8	LJ	7.2	4	5-10	7.4	5	6-9
	Trans	UJ	7	1		7	1	
	10.3	LJ	>9	1		>9	1	

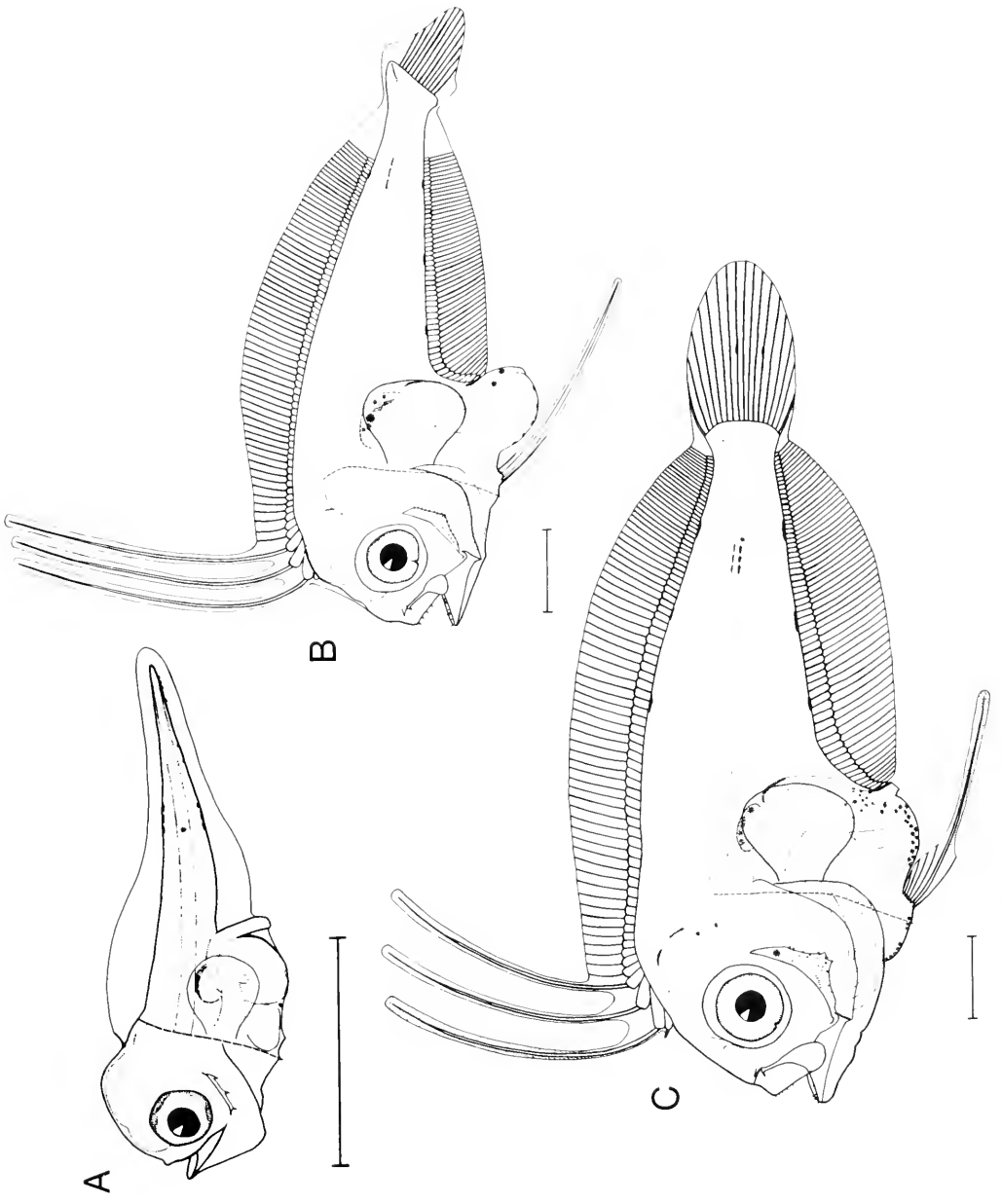


FIGURE 4.—Larval stages of *Citharichthys cornutus*: A. Preflexion, 2.2 mm; B. Midflexion, 6.9 mm; C. Late flexion, 8.2 mm. Scale = 1 mm.

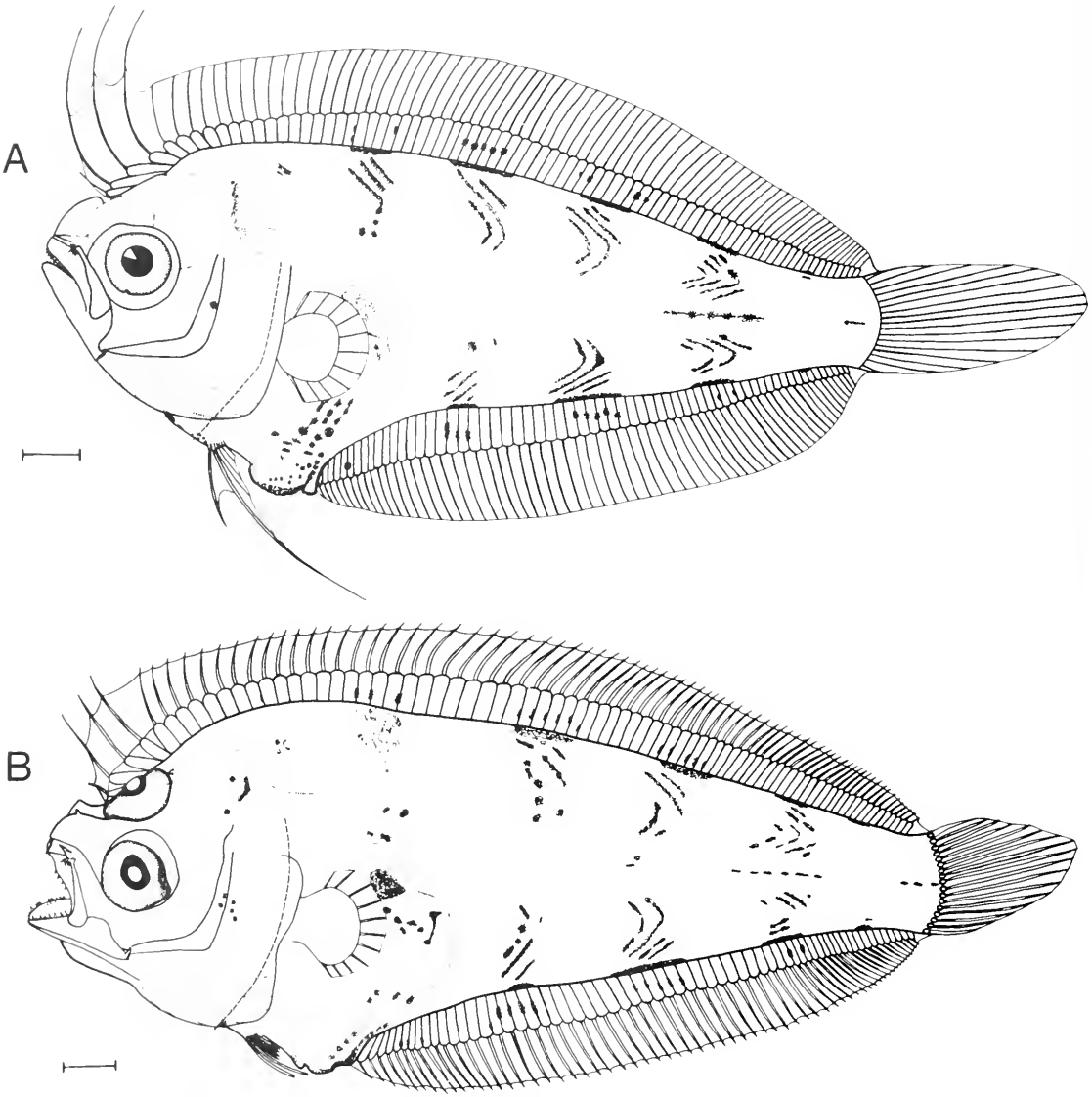


FIGURE 5.—*Citharichthys cornutus*: A. Transforming larva, 14.2 mm; B. Nearly transformed larva, 17.4 mm; C. Adult, 37.2 mm. Scale = 1 mm.

Surface temperature and salinity were 20.4°-27.3°C and 35.5-36.8 ‰. Almost no larvae were caught east of the average Gulf Stream axis (Fig. 1). The reported northern limit for adults is Florida (with one exception— an adult male taken off Cape Hatteras (Stewart[5])). Larval occurrences shown in Figure 1 are evidence of the effectiveness of Gulf Stream transport. The eastward shift of positive tows just north of lat. 32°N corresponds to the location of a semipermanent meander of the Gulf Stream induced by the Charleston Rise (at about lat. 32°N, long. 79°W (Pietrafesa et al. 1978)).

In the eastern Gulf of Mexico, larvae smaller than 4 mm NL were common in January, February, May, June, July, August, and November, indicating year-round spawning in that area (Dowd 1978).

[5]D. J. Stewart, Graduate Student, Laboratory of Limnology, University of Wisconsin, Madison, WI 53706, pers. commun. June 1978.

Citharichthys gymnorhinus (Figs. 1, 6, 7)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (15)
Caudal vertebrae = 23(3)-24(18)
Gill rakers (lower limb, first left) = ~12 (1)
Left pelvic rays = 5 (12)
Anal rays = 55-59 (11)
Dorsal rays = 70-75 (11)

Of the potential species listed in Table 1, only *C. gymnorhinus* has counts that agree with these (it is unique in having only five left pelvic rays). In addition, larvae were captured over the outer shelf, but not as far offshore as *C. cornutus* (Fig. 1). This is consistent with bathymetric distribution of adults.

Distinguishing Characters

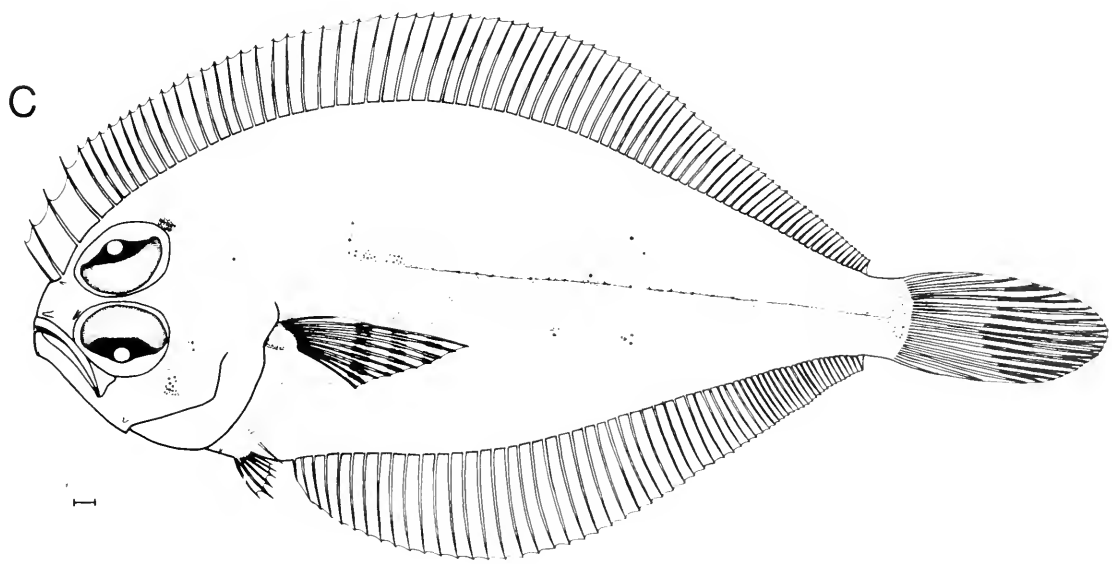
Citharichthys gymnorhinus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Three elongate dorsal rays are present from preflexion (4.6 mm) through postflexion (probably through transformation). Caudal vertebrae (23-24) can be counted by early flexion (6 mm). Lateral pigment is relatively sparse except for the caudal band. Flexion is complete at 7-8 mm SL. Morphology is similar to that of *C. cornutus*. However, the left pelvic fin of *C. gymnorhinus* has a full complement of only five rays, and in larvae the first ray is much reduced in size compared with that of *C. cornutus*. Length of *C. gymnorhinus* at transformation is probably about 18 mm. Larvae may appear in collections year-round.

Pigmentation

Pigmentation of *C. gymnorhinus* larvae is moderate. Gas bladder and caudal band pigment are the most striking.

By 4.6 mm and throughout larval development, the dorsal one-third of the left side of the gas bladder is fairly heavily pigmented, usually with distinct melanophores. With growth, the number of melanophores increases. There are usually more of them than in *C. cornutus* larvae. The maximum number in a preflexion specimen was about 15 (4.6 mm, Fig. 6A). The right side of the gas bladder is either unpigmented or has only one or two melanophores.

By 4.6 mm (Fig. 6A) a caudal band of melanophores is present on the dorsal and ventral finfolds and sides and margins of the body about halfway from the anus to the notochord tip. This band is more distinct and regular than in other



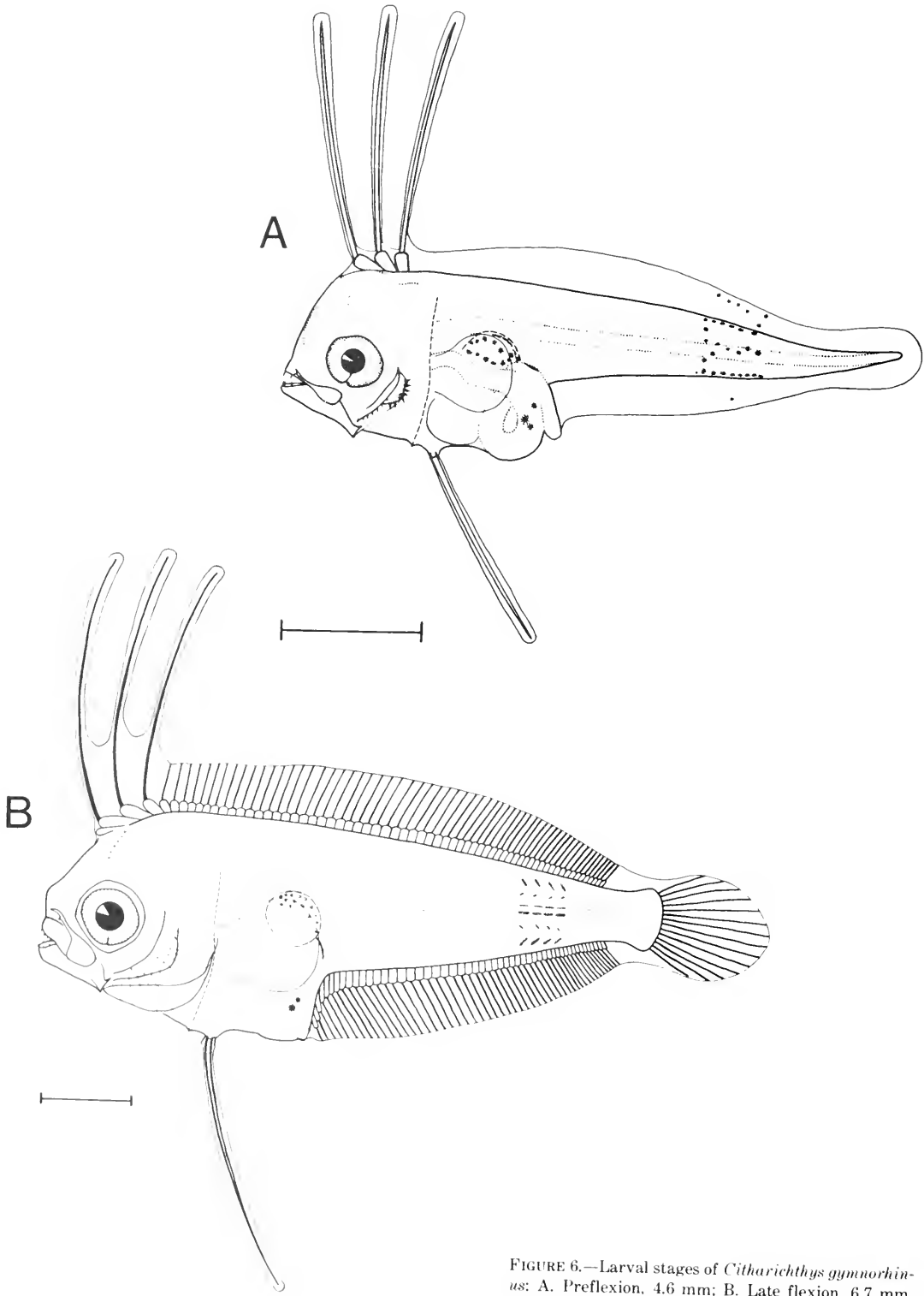


FIGURE 6.—Larval stages of *Citharichthys gymnorhinus*: A. Preflexion, 4.6 mm; B. Late flexion, 6.7 mm. Scale = 1 mm.

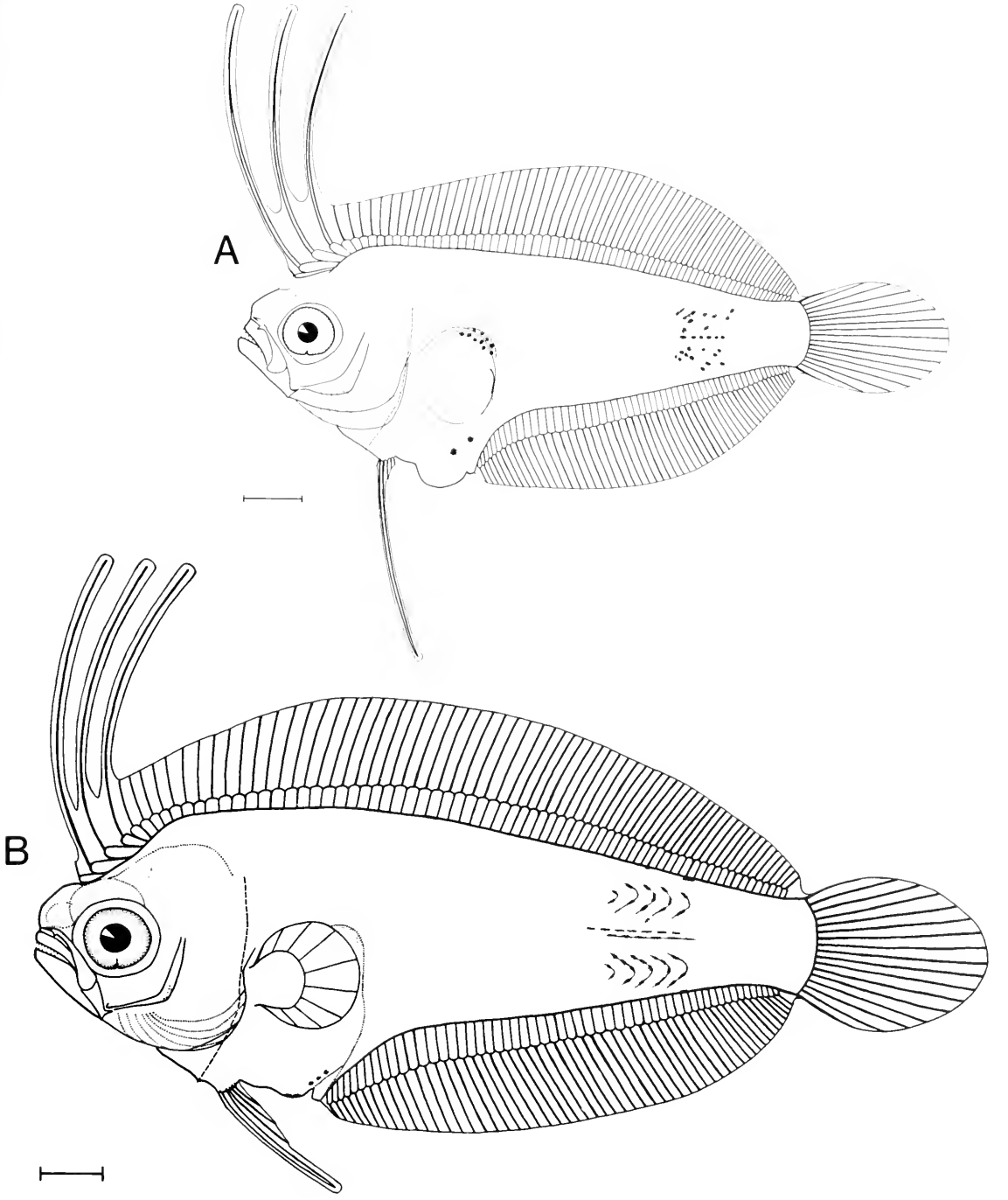


FIGURE 7.—Larval stages of *Citharichthys gymnorhinus*: A. Transforming, 9.6 mm; B. Transforming, 12.6 mm. Scale = 1 mm.

known larvae of western North Atlantic *Citharichthys* and *Etropus* species. In preflexion larvae, before pelvic rays form, one or two melanophores are present on the ventral body margin at the future site of the pelvic fin. By 4.6 mm and throughout development (at least to 13 mm), a few external melanophores are present along the posterior surface of the gut loop. A small melanophore is found over the posterodorsal surface of the midgut of preflexion larvae.

Flexion larvae (Fig. 6B) usually have 15-20 melanophores on the dorsal one-third of the left side of the gas bladder. The caudal band is mostly confined to the body and contains myoseptal pigment. Visible internal notochordal pigment is restricted to the vicinity of the external caudal band. The dorsal surfaces of one or two forming centra are darkened at about 5 mm. By about 6 mm and throughout development (at least to 13 mm), there may be a few melanophores along the ventral surface of the gut loop. By late flexion, notochordal pigment appears as fine dashes along four to six centra of caudal vertebrae 13-19. By late flexion, pigment along the posterodorsal surface of the midgut extends to the gas bladder and appears as a black lining over the gut.

By postflexion (about 8 mm, Fig. 7A), both sides of the gas bladder usually are obscured by body musculature, and pigment in this area appears diffuse. Small melanophores appear on the left pelvic fin membrane along both sides of the elongate second ray. Body musculature tends to obscure notochordal pigment in larvae longer than 12 mm.

Morphology (Figs. 6, 7; Tables 3, 6)

General morphological features are similar to those of *C. cornutus*, with the qualification that the smallest *C. gymnorhinus* specimen examined was 4.6 mm NL. Adult morphometrics given in the following discussion were derived from Gutherz and Blackman (1970) and Topp and Hoff (1972).

The mouth is relatively large in larvae and adults. Larval upper jaw length/BL is fairly constant at 9.3-9.5%. Adult upper jaw length/BL is 11.2%, range 9.9-13.0%. Larval upper jaw length/HL decreases greatly from 38% (preflexion) to 33% (flexion and postflexion). Adult upper jaw length/HL is 41%, range 39-45%. Larval lower jaw length/BL increases from 11.5% to 12.7%. Adult lower jaw length/BL is 13.2%, range 11.6-14.8%. Larval lower jaw length/HL decreases slightly from 46% to 44% and is only slightly less than that of *C. cornutus*. Adult lower jaw length/HL is 48%, range 43-53%.

The larval snout is pointed but relatively short. Larval snout length/BL increases slightly from 5.2% to 6.1%. Adult snout length/BL is 5.4%, range 4.6-6.6%. Larval snout length/HL is constant at 21%. Adult snout length/HL is 20%, range about 18-20%.

The eye is relatively large in larvae and adults (only slightly smaller than that of *C. cornutus*). Larval eye diameter/BL is constant at about 8.8%. Adult orbit length/BL is 9.6%, range 8.0-11.4% (Topp and Hoff 1972); eye diameter/BL is 10.1%, range 9.1-11.0% (Gutherz and Blackman 1970). Larval eye diameter/HL decreases from 35% to 31% and is similar to that of *C. cornutus*. Adult orbit length/HL is 35% (Topp and Hoff 1972); eye diameter/HL is 36.5%, range 33-38% (Gutherz and Blackman 1970).

The head is fairly long but shallow in larvae and of moderate length in adults. Larval head length/BL increases greatly from 25% to 29%. Postflexion head length/BL is similar to those of *C. arctifrons* and *C. cornutus*. Adult head length/BL is 27%, range 25-29%. Larval head depth/BL increases from 29% to 33% and is similar to that of *E. crossotus*.

Larval snout to anus length is fairly great until postflexion. Snout to anus length/BL increases slightly from 43% (preflexion) to 44% (flexion) and then decreases to 40% (postflexion). This length is similar to that of *E. crossotus* during flexion and postflexion.

With the exception of a relatively deep caudal peduncle, the body is of moderate depth in larvae and adults. Larval body depth at pelvic fin/BL increases from 30% to 39%. Larval body depth at loop of gut/BL increases from 29% to 44%. Larval body depth at anus/BL increases greatly from 25% to 42% and during flexion and postflexion is similar to that of *E. crossotus*. Larval body depth at third hemal spine/BL increases greatly from 14% to 35%. Adult body depth/BL is 47%, range 39-50%. Larval caudal peduncle depth/BL increases from 11.6% (flexion) to 13.2% (postflexion). Adult caudal peduncle depth/BL is 11.5%, range 10.5-12.6%.

Fin and Axial Skeleton Formation

Caudal skeleton development is similar to that of *C. cornutus*. Size ranges of available speci-

TABLE 6.—Measurements (mm) of larvae of *Citharichthys gymnorhinus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at loop of gut	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
4.4	0.45	0.53	0.24	0.42	1.2	1.9	4.6	1.2	[1]1.4	[1]1.4	[1]1.2	[1]0.69		ECF	S
4.5	0.41	0.49			1.1	2.0				[1]1.3	[1]1.0	[1]0.53		Pref	S
4.6	0.38	0.50	0.21	0.40	1.1	2.1	4.6	1.4	[1]1.3	[1]1.3	[1]1.1	[1]0.60		ECF	S
4.6	0.44	0.56	0.25	0.39	1.1	2.0		1.2	[1]1.3	[1]1.3	[1]1.1	[1]0.64		Pref	S
4.6	0.43	0.47	0.17	0.42	1.1	2.0	4.7	1.4	[1]1.2	[1]1.2	[1]1.1	[1]0.59		Pref	S
5.0	0.52	0.65	0.34	0.41	1.3	2.1	5.1	1.5	1.7	1.7	1.5	0.92		ECF	S
5.3	0.50	0.66	0.26	0.52	1.3	2.4		1.7	1.8	1.9	1.6	1.1		Early	S
5.9	0.55	0.73	0.31	0.51	1.5	2.4		1.7	1.9	1.9	1.8	1.2		Early	S
6.0	0.50	0.70	0.30	0.42	1.5	2.5	6.2	1.7	2.0	2.0	2.0	1.2		Early	S
6.4	0.59	0.86	0.43	0.54	1.8	2.9		2.2	2.4	2.7	2.3	1.6	0.67	Mid	S
6.6	0.61	0.85	0.36	0.63	1.9	3.0		2.3	2.5	2.8	2.5	1.9		Mid	S
6.6	0.60	0.79	0.37	0.58	1.8	2.9		2.1	2.3	2.3	2.2	1.6	0.64	Mid	2
6.7	0.63	0.84	0.40	0.59	1.9	2.8		2.3	2.5	2.4	2.4	1.8	0.70	Late	S
6.8	0.63	0.83	0.41	0.60	1.8	2.9		2.3	2.6	2.8	2.6	1.8	0.76	Late	2
6.7	0.65	0.90	0.38	0.60	1.9	3.2			2.7	3.0	2.7	2.0	0.82	Late	1
6.9	0.63	0.83	0.38	0.59	1.9	3.2		2.2	2.5	2.5	2.3	1.6	0.64	Late	2
7.2	0.67	0.98	0.44	0.72	2.2	3.1	8.6	2.5	2.9		3.0	2.3	0.94	Late	1
7.2	0.69	0.94	0.40	0.63	2.1	3.3		2.6	2.9	3.0	2.9	2.1	0.90	Late	1
7.2	0.72	0.96	0.51	0.62	2.1	3.2		2.4	2.7	2.8	2.7	2.0	0.84	Late	1
7.5	0.68	0.99	0.49	0.67	2.3	3.5		2.7	3.1	3.4	3.3	2.5	1.0	Late	2
7.7	0.72	0.99	0.48	0.77	2.3	3.5	9.7	2.8	3.3	3.4	3.2	2.5	1.1	Late	2
7.9	0.79	1.1	0.50	0.73	2.7	3.4		2.8	3.3	3.6	3.4	2.6	1.0	Post	1
8.2	0.93	1.2	0.63	0.81	2.6	3.8	9.9	3.0	3.6	4.1	3.9	2.9	1.2	Post	3
8.3	0.75	1.0	0.47	0.74	2.3	3.4		2.9	3.2	3.4	3.3	2.4		Post	2
8.6	0.80	1.1	0.47	0.78	2.4	3.6	10.4	3.0	3.4	3.6	3.5	2.7	1.1	Post	2
9.0	0.83	1.2	0.52	0.77	2.6	3.7		3.2	3.6		3.9	3.2	1.3	Post	3
9.6	0.94	1.3	0.64	0.87	2.8	3.9	11.6	3.2	3.8	4.3	4.1	3.4	1.3	Post	2
9.8	0.91	1.3	0.63	0.84	2.8	4.1		3.2	3.8	4.3	4.2	3.4		Post	2
9.8	0.92	1.2	0.60	0.87	2.8			3.1	3.8			3.3	1.2	Post	3
9.9	0.85	1.2	0.60	0.84	2.8	4.0	12.0	3.3	3.7	4.2	4.0	3.1	1.3	Post	2
10.2	0.94	1.2	0.63	0.92	2.8	4.2	12.5	3.5	4.0	4.5	4.4	3.5	1.3	Post	3
10.4	0.93	1.3	0.50	0.95	2.8	4.2		3.6	3.9	4.4	4.3	3.5	1.4	Post	3
10.6	0.98	1.4	0.71	0.87	3.1	4.0			4.2	4.6	4.5	3.9	1.5	Post	2
11.2	1.0	1.4	0.54		3.1	4.2		3.6	4.4	4.9	4.8	4.0	1.5	Post	2
11.7	1.2	1.4	0.74	0.99	3.2	4.5		3.7	4.5	5.0	4.9	4.0	1.5	Post	3
11.7	0.95	1.5	0.70	0.92	3.2	4.0		3.7	4.4	5.2	4.9	4.4	1.4	Post	3
12.6	1.1	1.6	0.73	1.1	3.5	4.6	15.3	4.0	4.9		5.2	5.3	1.7	Post	3
12.9	1.2	1.7	0.84	1.2	3.6	4.8		4.2	5.0	5.7	5.5	4.8	1.6	Post	3
12.9	1.2	1.6	0.78	1.1	3.7	4.5		4.0	4.8	5.4	5.2	4.7	1.7	Post	3
12.9	1.1	1.5	0.82	1.0	3.6	5.0	15.8	4.1	4.7	5.8	5.5	4.4	1.7	Post	2

[1]Measurement does not include dorsal or anal pterygiophores

mens in each stage are as follows: Preflexion, 4.5-5.4 mm NL; early caudal formation, 4.4-5.3 mm NL; early flexion, 5.3-6.0 mm NL; midflexion, 6.0-6.6 mm NL; late flexion, 6.7-7.7 mm NL; postflexion, 7.9-12.9 mm SL. Caudal rays become calcified between early flexion (5.9 mm NL) and late flexion (7.2 mm NL).

All precaudal neural spines stain with alizarin by about 6.0 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.6 mm NL, and all do by 6.0 mm NL. All precaudal centra stain with alizarin by about 6.7 mm NL. All caudal centra, including the urostyle, stain with alizarin by about 7.2 mm NL. The smallest specimen in which caudal centra could be counted was 6.1 mm NL (early flexion). The second, third, and fourth dorsal rays are elongate and widely separated at the bases from preflexion (4.4 mm NL) through postflexion (12.9 mm SL). During early caudal formation (5.0 mm NL) rays near the middle of the fin begin to calcify.

Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 7.0 mm NL) onward. The first ray and the most posterior rays are probably calcified prior to transformation.

During early caudal formation (5.0 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from midflexion (about 6.6 mm NL) onward. The most

posterior rays are probably calcified by the time transformation is complete.

Development of the left pelvic fin precedes that of the right fin. The left pelvic fin bud appears during preflexion (before 4.5 mm NL, probably at about 4.0 mm NL). Rays develop between preflexion (about 4.5 mm NL) and postflexion (7.9 mm SL). The second ray is the first to appear (4.5 mm NL); it is elongate. (This ray may actually be the result of fusion of the second and third rays.) The first ray does not appear until early flexion (5.9 mm NL). It is weak, never elongate, and usually the shortest ray in the fin. The right pelvic fin bud appears during early flexion (5.3 mm NL). Rays develop between late flexion (6.7 mm NL) and postflexion (about 9.0 mm SL). There are five rays in the complete left fin and six in the right.

Rayless, fanlike, larval pectoral fins were present on the smallest available specimen (preflexion, 4.4 mm NL). Calcification of rays in the left fin begins during postflexion (about 11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (4.4 mm NL). With development (Figs. 6A, B, 7A), additional spines appear until maximum numbers of about 31 on the left side (range 25-38) and 39 on the right side (range 34-43) are reached during postflexion (8.3-10.2 mm SL). The largest specimen (12.9 mm SL) has only about three left (uncertain count) and seven right spines. Most are probably lost by transformation.

Frontal-sphenotic spines were evident in the smallest preflexion specimen (4.4 mm NL) and throughout the larval series, though less conspicuous in larger specimens (10-13 mm SL). The lowermost spine on the left side is usually just above the center of the eye and on the right side slightly anterior to the center of the eye. (During transformation those on the right side are at the anterior margin of the skull.) The spines are arranged in a slightly posteriorly concave arch following the curve of the skull. There are usually six (maximum of six) per side, including three stronger spines arising from a small bulge of the skull.

Larval Teeth (Table 5)

Numbers of teeth of preflexion (4.5-5.4 mm NL) larvae range from two upper and two lower to three upper and four lower on each side. During early caudal formation (4.6-5.3 mm NL), numbers range from two upper and three lower to three upper and four lower on each side. During early flexion (5.3-6.0 mm NL), teeth increase from two upper and four lower to four upper and five lower on each side. During midflexion (6.4-6.6 mm NL), there are four or five upper and five or six lower teeth on each side. During late flexion (6.7-7.7 mm NL), teeth increase from four upper and six lower to seven upper and eight lower on each side. During postflexion (7.9-12.9 mm SL), teeth increase from about six upper and six lower on each side to about eight upper on both sides, more than nine in the lower left jaw, and more than eight in the lower right jaw.

Transformation

Migration of the right eye may begin as early as midflexion (6.6 mm NL) or as late as postflexion (7.9 mm SL). The right eye moves from the right side of the head through a space between the dorsal fin and supraorbital bars (Fig. 7B) as in *Cyclopsetta fimbriata* (Gutherz 1971). The right eye probably reaches its final position on the left side of the head by about 18 mm SL. No early juvenile specimen was available. This size is based on a transformation rate similar to that of *Citharichthys cornutus* and a 16.0 mm SL specimen of *C. gymnorhinus* in which the right eye was about halfway to the dorsal ridge.

Occurrence

Larvae were collected in the Atlantic during February, March, April, May, and October (Powles footnote 4). There was no apparent size progression by month, indicating an extended spawning season. Water depth was 14.6-446 m. Surface temperature and salinity were 19.0°-26.5°C and 33.8-37.0‰. *Citharichthys gymnorhinus* larvae occurred slightly closer to shore and not quite as far north as those of *C. cornutus*. The reported northern limit for adult *C. gymnorhinus* is Georgia. (See *C. cornutus*, section on Occurrence.)

In the eastern Gulf of Mexico, larvae smaller than 4 mm NL were common in January, February, May, June, July, August, and November, indicating year-round spawning in that area (Dowd 1978).

Citharichthys spilopterus (Figs. 8, 9)

Identification

Most specimens had complete complements of countable characters. They were identified by comparing the following larval and juvenile counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (40)
Caudal vertebrae = 23(16), 24(38), 25(6)
Gill rakers (lower limb, first left) = 11-14 (9)
Left pelvic rays = 6 (24)
Anal rays = 55-62 (53)
Dorsal rays = 74-82 (53)

Of the potential species listed in Table 1, only 3 have 23-24 caudal vertebrae (Append. Table 1). *Citharichthys gymnorhinus* has only five left pelvic rays, and lower anal and dorsal fin ray counts. *Etropus rimosus* has 3-7 gill rakers and usually only 24-25 caudal vertebrae. In addition, most larvae were caught in an estuary, which is consistent with *C. spilopterus* adult distribution.

Distinguishing Characters

Citharichthys spilopterus larvae have no pectoral melanophore, and notochordal pigment is restricted to the caudal region. Two elongate dorsal rays are present from preflexion (3.7 mm) through transformation. Caudal vertebrae (23-24, rarely 25) can be counted by late flexion (5.7 mm). Lateral larval pigmentation is relatively light, but juvenile pigmentation is heavy. Flexion is complete at 7-8 mm SL. The larval snout is very blunt and the body is deep. Relative snout to anus length is small. The left pelvic fin has a full complement of six rays. Length at transformation is 9-11 mm. Larvae usually appear in collections from September through April.

Pigmentation

Pigmentation of *C. spilopterus* larvae is relatively light, but it becomes heavy in juveniles. Gas bladder, lower gut, and lateral tail pigment are the most striking.

By about 3.7 mm (early caudal formation, Fig. 8A) and throughout larval development, the left side of the gas bladder is fairly heavily pigmented, usually with one or two distinct melanophores. No pigment is evident on the right side of the gas bladder. Additional melanophores sometimes appear later in development, but are usually larger and fewer in number than in the preceding two species. The only other pigment apparent in the 3.7 mm specimen is a small amount along the ventral surface of the gut loop.

During late flexion (6.7 mm, Fig. 8B), two dashlike melanophores are present on the ventral body margin between the anus and the caudal fin base. A few melanophores appear on each side of the symphysis of the lower jaw. A melanophore is on the posterior margin of the articular. Pigment along the ventral surface of the gut loop increases. Some pigment may occur on the ventral body margin anterior to the cleithrum. A stellate melanophore is present at the junction of left and right branchiostegal membranes, just forward of the isthmus. A series of small melanophores usually is present along the distal tips of anal pterygiophores.

During postflexion, one to five (usually one or two) melanophores are present on the left side of the gas bladder. Additional dashlike clusters of pigment (up to four total) appear on the ventral body margin along the anal fin base, but the first two remain the most distinct (8.7 mm). Similar clusters of pigment appear on the dorsal body margin along the dorsal fin base (up to six from above the hindbrain to the caudal fin base). Heavy pigment is present along the ventral body margin anterior to the cleithrum. The area immediately around the anus is usually densely pigmented internally. Several external melanophores are present on the body below the pectoral fin base and along the ventral and lateral surfaces of the abdomen. Internal melanophores are present along the hindgut. Visible internal notochordal pigment is restricted to a small area just forward of the caudal peduncle. This appears as fine dashes along the dorsal surfaces of one to a few centra in the area of caudal vertebrae 15-16. Some internal pigment is present near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (visible through the opercle). The left pelvic fin becomes pigmented, mostly around the first to third rays. Clusters of melanophores appear on the dorsal and anal fins. Often, melanophores occur along the sides of the middle caudal rays. By about 9 mm, lateral melanophores appear on the snout, jaws, and posterior part of the head. One or two internal melanophores appear above the brain.

Gas bladder pigment becomes diffuse after

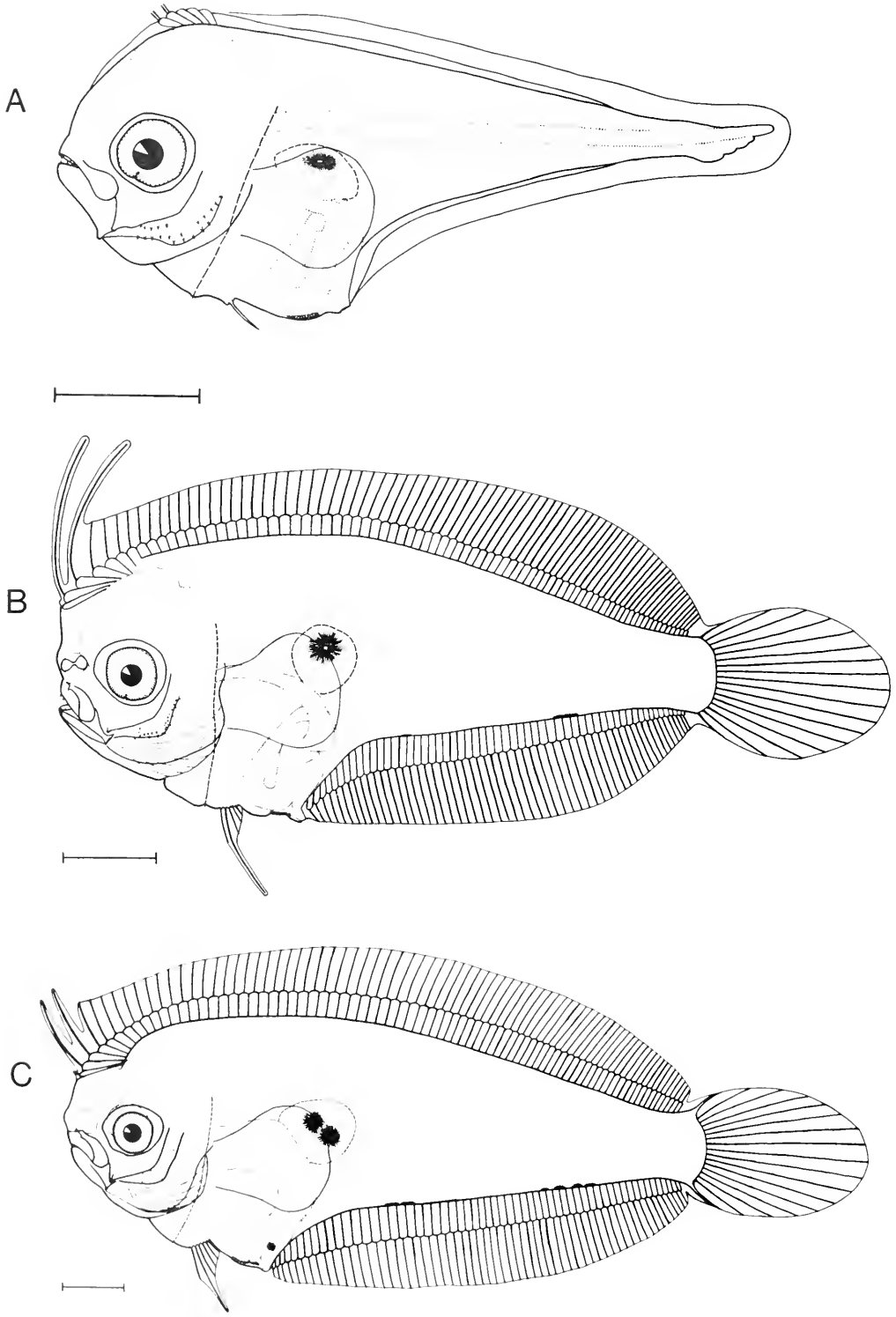


FIGURE 8.—Larval stages of *Citharichthys spilopterus*: A. Preflexion (early caudal formation), 3.7 mm; B. Late flexion, 6.7 mm; C. Transforming, 9.9 mm. Scale = 1 mm.

transformation and is obscured by body musculature in most specimens longer than 10 mm. A caudal band does not appear until the myoseptal pigment pattern of early juveniles is established (9-10 mm, Fig. 9B). By the end of transformation, myoseptal pigment is well developed, mostly adjacent to dorsal and anal pigment clusters; it often forms additional vertical bands across the body. In older juveniles (16 mm, Fig. 9C), the dorsal and anal clusters and myoseptal pigment become less distinct and partially blend in with the increasing brownish ground color.

Morphology (Figs. 8, 9; Tables 3, 7)

General morphological features are similar to those of *C. cornutus*, with the qualification that the smallest *C. spilopterus* specimen examined was 3.7 mm NL. Adult morphometrics given in the following discussion were derived from Gutherz (1967) and Dawson (1969).

During flexion and postflexion, the mouth is relatively small and is similar in size to that of *E. crossotus*. The adult mouth is also small for the genus. Upper jaw length/BL decreases greatly from 9.9% (preflexion) to 6.7% (postflexion) and then increases greatly to 9.0% (midjuvenile). Adult upper jaw length/BL is 10.5%. Upper jaw length/HL decreases greatly from 36% (preflexion) to 27-29% (flexion to early juvenile) and then increases greatly to 36% (midjuvenile). Adult upper jaw length/HL is about 37%, range 31-40%. Lower jaw length/BL decreases greatly from 12.1% (preflexion) to 9.1% (postflexion) and then increases greatly to 13.1% (midjuvenile). Adult lower jaw length/BL is 12.4%. Lower jaw length/HL decreases greatly from 43% (preflexion) to 38% (flexion and postflexion) and then increases greatly to 53% (midjuvenile). Adult lower jaw length/HL is 44%, range 41-47%.

The larval snout is relatively long but blunt. The adult snout is relatively pointed. Snout length/BL decreases from 7.5-7.6% (preflexion and flexion) to 6.4% (postflexion) and 5.0% (midjuvenile). Adult snout length/BL is 5.6%. Snout length/HL is fairly constant at 27-29% from preflexion through postflexion and then decreases to 20% (midjuvenile). Adult snout length/HL is 20%, range 18-22%.

The eye is moderate in larvae and small in adults. Eye diameter/BL decreases greatly from 9.7% (preflexion) to 6.5% (postflexion) and then increases slightly to 7.0% (midjuvenile). Postflexion eye diameter/BL is similar to those of *E. crossotus* and *E. microstomus*. Adult orbit diameter/BL is 5.6%. The large decrease in larval eye diameter/BL is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae. Eye diameter/HL decreases greatly from 35% (preflexion) to 27-28% (postflexion to midjuvenile). Adult orbit diameter/HL is 20%, range 13-25%.

The head is very blunt, with a nearly vertical anterior profile, prior to transformation. It is relatively long during preflexion, moderate during flexion, short during postflexion, and moderate in adults. Head length/BL decreases greatly from 28% (preflexion) to 24% (postflexion) and then increases to 25% (early and midjuvenile). Adult head length/BL is 28%, range 26-31%. The decrease in relative larval head length is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae. The head is relatively deep during preflexion and flexion, and shallow during postflexion. Head depth/BL increases from 37% (preflexion) to 39% (flexion), then decreases greatly to 33% (postflexion) and 31% (midjuvenile). Postflexion head depth/BL is similar to those of *C. gymnorhinus* and *E. crossotus*.

Snout to anus length is relatively short. Snout to anus length/BL decreases greatly from 39-40% (preflexion and flexion) to 31-32% (postflexion to midjuvenile).

The body is deep throughout the larval stages, except that the abdomen becomes only moderately deep by postflexion. During postflexion, the dorsal and ventral profiles are not as convex as in other known western North Atlantic *Citharichthys* and *Etropus* larvae. Adult body depth is moderate. Body depth at pelvic fin/BL increases from 40% (preflexion) to 47% (flexion) and then decreases to 39% (postflexion) and 35% (midjuvenile). Body depth at anus/BL increases from 39% (preflexion) to 51% (flexion) and then decreases to 43% (postflexion) and 39% (midjuvenile). Body depth at third hemal spine/BL increases from 23% (preflexion) to 41% (flexion), decreases to 37% (early juvenile), and then increases to 40% (midjuvenile). Adult body depth/BL is 46%, range 40-51%. Caudal peduncle depth/BL decreases from 14.4% (preflexion) to 13.5% (postflexion) and 11.4% (midjuvenile). Adult caudal peduncle depth/BL is 12.8%, range 11.0-13.9%. The decrease in relative larval caudal peduncle depth is exceptional among known western North Atlantic *Citharichthys* and *Etropus* larvae.

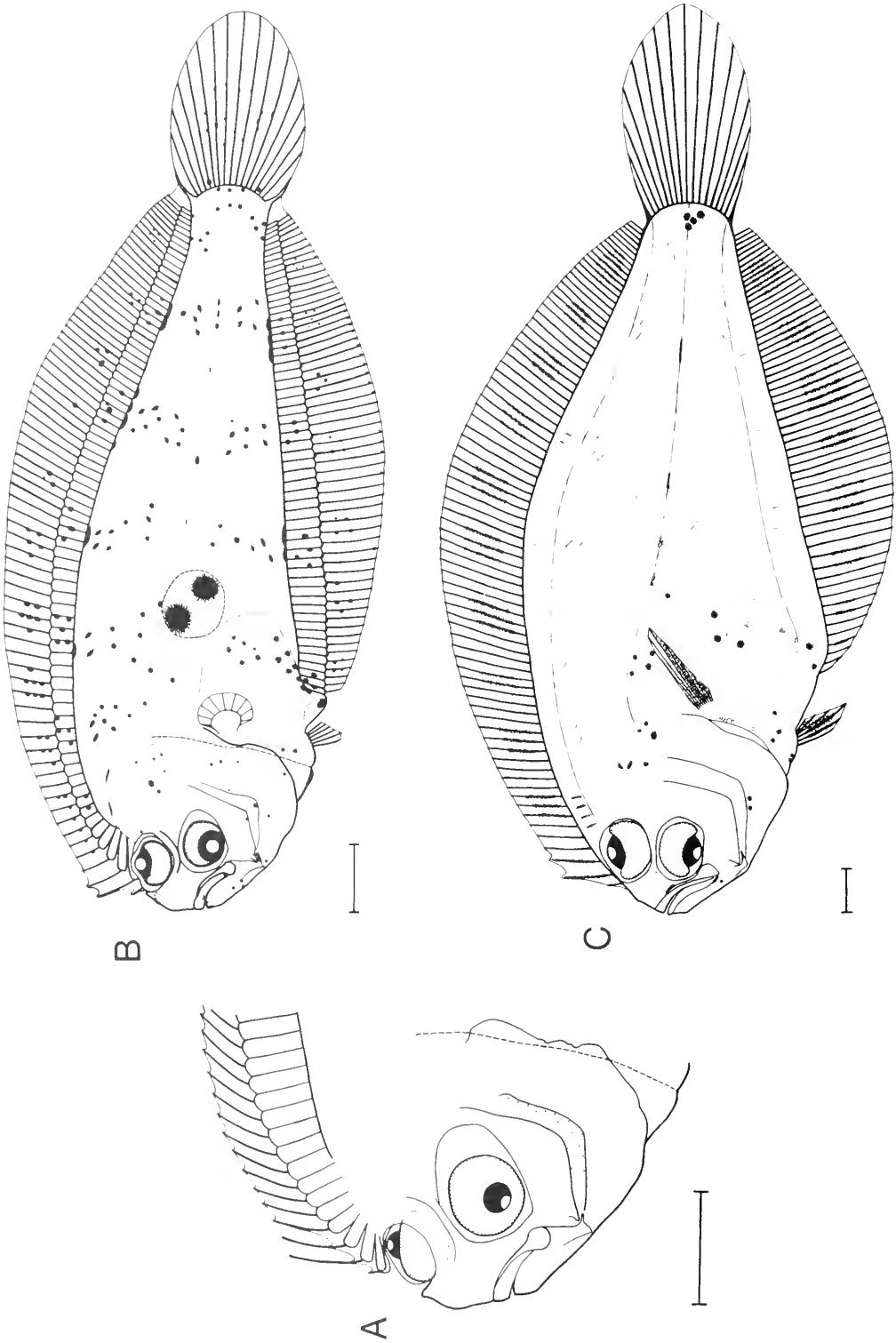


FIGURE 9.—*Citharichthys spilopterus*: A. Head of 9.9 mm larva showing migration of right eye around origin of dorsal fin (pigment omitted); B. Early juvenile, 10.7 mm; C. Juvenile, 16.6 mm. Scale = 1 mm.

TABLE 7.—Measurements (mm) of larvae and juveniles of *Citharichthys spilopterus*. ECF = early caudal formation, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, R = on the dorsal ridge, T = transformed.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
3.7	0.37	0.45	0.28	0.36	1.0	1.5	3.8	1.4	[1]1.5	[1]1.4	[1]0.84		ECF	S
5.7	0.42	0.58	0.46	0.46	1.5	2.2		2.4	2.7	2.9	2.2	0.74	Late	S
6.7	0.42	0.61	0.53	0.51	1.7	2.5	8.5	2.5	3.1	3.3	2.6	0.93	Late	S
6.8	0.54	0.71	0.46	0.54	1.8	2.7		2.6	3.2	3.5	3.0	1.1	Late	1
8.3	0.66	0.80	0.55	0.53	2.0	2.7	10.4	2.8	3.4	3.7	3.2	1.2	Post	3
8.7	0.66	0.88	0.53	0.54	2.3	2.8	11.3	3.0	3.5	3.8	3.4	1.3	Post	T
8.9	0.54	0.83	0.50	0.52	2.0	3.0	11.1	3.0	3.6	4.0	3.5	1.2	Post	1
8.9	0.61	0.82	0.61	0.56	2.1	2.9	11.0	3.0	3.6	4.0	3.4	1.2	Post	2
8.9	0.65	0.85	0.50	0.63	2.2	2.9	11.1	3.1	3.5	3.8	3.4	1.3	Post	R
9.0	0.73	1.0	0.58	0.58	2.4	2.9	11.7	3.1	3.5	3.6	3.4	1.2	Post	T
9.0	0.62	0.81	0.60	0.58	2.2	2.8	11.0	3.0	3.6	4.0	3.6	1.2	Post	S
9.1	0.58	0.80	0.56	0.60	2.1	2.9	11.3	3.0	3.4	3.6	3.3	1.2	Post	3
9.1	0.70	0.90	0.65	0.60	2.4	3.1	11.2	2.9	3.3	3.4	3.1	1.2	Post	T
9.1	0.67	0.93	0.56	0.60	2.3	3.0	11.2	2.9	3.3	3.5	3.3	1.3	Post	T
9.2	0.70	0.93	0.58	0.70	2.4	2.8	11.4	3.2	3.7	3.9	3.6	1.3	Post	R
9.2	0.64	0.97	0.46	0.64	2.3	2.7	11.4	2.9	3.6	3.8	3.4	1.3	Post	T
9.2	0.67	0.87	0.60	0.62	2.4	2.8	11.4	3.0	3.6	3.8	3.5	1.3	Post	T
9.2	0.68	0.89	0.62	0.60	2.3	2.8	11.2	2.9	3.4	3.9	3.2	1.3	Post	R
9.3	0.57	0.80	0.56	0.60	2.2	2.9	11.4	3.0	3.6	3.9	3.4	1.2	Post	1
9.3	0.67	0.90	0.65	0.63	2.4	2.9	11.7	3.0	3.4	3.8	3.7	1.3	Post	T
9.4	0.68	0.93	0.53	0.68	2.4	2.7	11.7	3.0	3.5	3.7	3.4	1.3	Post	T
9.4	0.69	1.0	0.56	0.68	2.3	3.0	11.6	3.1	3.5	3.7	3.8	1.4	Post	T
9.4	0.67	0.94	0.59	0.67	2.4	2.9	11.7	2.9	3.4	3.7	3.3	1.3	Post	T
9.5	0.71	1.0	0.60	0.68	2.4	3.1	11.8	3.0	3.6	3.8	3.4	1.3	Post	T
9.6	0.66	0.91	0.71	0.53	2.3	3.1	12.0	3.3	3.8	4.1	3.8	1.4	Post	R
9.7	0.69	0.93	0.64	0.68	2.5	2.9	11.8	3.2	3.6	3.9	3.6	1.3	Post	R
9.7	0.61	0.80	0.70	0.56	2.2	3.3	11.9	3.2	3.9	4.3	3.7	1.2	Post	S
9.8	0.65	0.89	0.58	0.74	2.4	3.2	11.9	3.1	3.8	4.1	3.6	1.2	Post	1
9.8	0.67	0.87	0.70	0.64	2.4	3.2	11.9	3.1	3.8	4.4	3.8	1.2	Post	1
10.0	0.72	1.0	0.54	0.72	2.5	3.0	12.2	3.2	3.6	3.8	3.6	1.3	Post	T
10.0	0.76	1.0	0.67	0.73	2.6	3.2	12.5	3.2	3.8	3.9	3.7	1.4	Post	T
10.0		1.1		0.73	2.5	3.0	12.2	3.2	3.7	4.0	3.6	1.3	Post	T
10.2	0.68	0.90	0.70	0.67	2.4	3.2	12.4	3.2	3.9	4.2	3.8	1.3	Post	3
10.2	0.71	1.0	0.56	0.64	2.6	3.1	12.5	3.1	3.5	3.7	3.6	1.4	Post	T
10.2	0.78	1.1	0.58	0.75	2.5	3.2	12.7	3.4	3.9	4.2	3.9	1.4	Post	T
10.2	0.73	1.1	0.53	0.76	2.6	3.2	12.5	3.3	3.8	4.0	3.8	1.4	Post	T
10.2		1.0	0.60	0.70	2.4	3.2	12.2	3.3	3.9	4.1	3.9	1.4	Post	T
10.3	0.83	1.1	0.64	0.64	2.6	3.2	12.7	3.4	3.8	4.1	3.8	1.4	Post	T
10.3	0.79	1.1	0.60	0.74	2.7	3.3	13.0	3.4	3.9	4.2	3.9	1.4	Post	T
10.5	0.76	1.1	0.60	0.71	2.6	3.4	13.0	3.4	3.8	4.2	4.0	1.4	Post	T
10.5	0.59	0.92	0.60	0.66	2.4	3.2	12.9	3.5	3.9	4.4	4.2	1.4	Post	R
10.6	0.73	1.1	0.63	0.68	2.7	3.2	13.1	3.4	4.0	4.2	4.0	1.4	Post	T
10.6	0.65	1.1	0.50	0.67	2.6	3.2	13.1	3.5	4.0	4.3	4.1	1.4	Post	T
10.6	0.60	0.90	0.64	0.60	2.5	3.2	13.0	3.4	4.1	4.5	4.1	1.4	Post	1
10.7	0.74	0.95	0.47	0.77	2.6	3.2	13.0	3.2	3.8	4.1	3.9	1.4	Post	T
10.8	0.82	1.1	0.65	0.72	2.7	3.3	13.3	3.2	3.9	4.2	3.8	1.4	Post	T
10.9	0.76	1.1	0.55	0.66	2.7	3.1	13.4	3.4	4.0	4.3	4.0	1.4	Post	T
10.9	0.75	1.1	0.62	0.67	2.8	3.2	13.3	3.3	4.0	4.3	4.0	1.4	Post	T
11.0	0.81	1.1	0.61	0.65	2.7	3.2		3.4	3.8	4.0	3.9	1.3	Post	T
11.6	0.84	1.3	0.61	0.89	3.1	3.8	14.3	3.7	4.2	4.5	4.4	1.5	Post	T
14.3	1.3	1.9	0.77	1.2	3.8	4.9	18.3	4.6	5.2	5.6	5.6	1.6	Post	T
16.6	1.6	2.3	0.91	1.3	4.4	5.3	21.0	5.5	5.9	6.6	7.0	1.7	Post	T
16.7	1.5	2.2	0.75	1.1	4.0	5.0		5.2	6.0	6.4	6.6	1.9	Post	T
19.4	1.7	2.5	0.84	1.3	4.8	6.0	24.1	5.8	6.7	7.5	7.8	2.2	Post	T
22.0	2.1	3.0	1.2	1.4	5.4	6.8	27.9	6.9	7.6	8.6	9.0	2.7	Post	T
23.1	1.9	2.9	1.1	1.6	5.6	7.1	28.5	7.0	7.7	8.6	9.0	2.7	Post	T
23.3	2.1	3.1	1.2	1.6	5.8	7.2	28.9	7.2	8.4	9.2	9.4	2.8	Post	T
24.0	2.2	3.1	1.1	1.6	6.0	7.8	30.0	7.4	8.3	9.2	9.7	2.6	Post	T
25.4	2.3	3.2	1.3	1.6	6.2	8.1	31.9	7.5	8.9	9.7		3.0	Post	T

[1]Measurement does not include dorsal or anal pterygiophores.

Fin and Axial Skeleton Formation

Caudal skeleton development apparently is similar to that of *C. cornutus*. Size ranges of available larval specimens in each stage are as follows: Early caudal formation, 3.7 mm NL; late flexion, 5.7-6.8 mm NL; postflexion, 9.0-10.6 mm SL. All caudal rays are calcified by 5.7 mm.

All precaudal neural spines, the first 13 caudal neural spines, the first 13 hemal spines, and no

precaudal or caudal centra stain with alizarin at 3.7 mm NL. All neural spines and hemal spines, some precaudal centra, and the urostyle stain with alizarin at 5.7 mm NL. All precaudal and caudal centra stain with alizarin at 6.7 mm NL. The smallest specimen in which caudal centra could be counted was 5.7 mm NL (late flexion).

The second and third dorsal rays are moderately elongate and moderately separated at the bases from preflexion (3.7 mm NL) through transformation (about 10 mm SL). No other dorsal rays were formed at 3.7 mm, but adult counts were present from 5.7 mm NL onward. All dorsal rays had calcified by postflexion (8.3 mm SL).

No anal rays were formed at 3.7 mm, but adult counts were present from 5.7 mm onward. All anal rays had calcified by 8.3 mm.

The second left pelvic ray is formed by 3.7 mm; in larger specimens it is elongate. By 5.7 mm, four left and four right pelvic rays are calcified. All six rays in each fin are calcified by 6.8 mm NL.

Rayless, fanlike, larval pectoral fins were present in the smallest specimen (3.7 mm). Calcification of rays in the left fin begins during postflexion (9-10 mm SL), and is complete by the end of transformation (9-11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present from early caudal formation (3.7 mm NL, Fig. 8A) through transformation (10.2 mm SL). Maximum numbers may be reached during or before late flexion (31 left, about 36 right); however, counts from early and midflexion larvae are lacking and those from older ones are highly variable. No preopercular spines are evident in juveniles.

The 3.7 mm NL specimen had one frontal-sphenotic spine on each side. Several postflexion (8-10 mm SL) specimens had one or two relatively inconspicuous frontal-sphenotic spines on each side. These spines may be more numerous in larvae smaller than 5.7 mm NL. None are evident in juveniles.

Larval Teeth (Table 5)

The early caudal formation (3.7 mm NL, Fig. 8A) specimen had two upper and three lower teeth on each side. During late flexion and postflexion (5.7-10.6 mm BL), larvae usually have four upper and five lower teeth on each side. Transforming larvae and early juveniles (9.1-10.7 mm SL) usually have about five upper left (probably about five upper right) and five or six lower left (probably five to eight lower right) teeth.

Transformation

Migration of the right eye may begin as early as late flexion (6.8 mm NL) or as late as postflexion (10.6 mm SL). The right eye moves from the right side of the head around the dorsal fin origin (Fig. 9A) as in *Citharichthys arctifrons* and *Etropus microstomus* (Richardson and Joseph 1973). The right eye reaches its final position on the left side of the head at about 9-11 mm SL.

Occurrence

Larvae were collected from September through December in the Gulf of Mexico off Texas (Daher[6]) and from October through April in the Cape Fear River estuary, North Carolina (pers. obs.). Temperature and salinity ranges at capture locations in the Cape Fear River were 4.1°-26.6°C and 0.0-31.7‰.

Etropus crossotus (Figs. 10, 11)

Identification

Larvae approaching transformation had complete complements of countable characters. Those specimens were identified by comparing the following larval counts with known adult counts. Number of specimens is given in parentheses.

Caudal fin formula = 4-5-4-4 (15)
Caudal vertebrae = 24(1), 25(19), 26(3)
Gill rakers (lower limb, first left) = ~7 (1)
Left pelvic rays = 6 (11)
Anal rays = 60-66 (13)
Dorsal rays = 76-84 (13)

Of the potential species listed in Table 1, only *E. crossotus* has counts that agree with these. In addition, most specimens were captured west of the Mississippi River in the Gulf of Mexico, an

[6]M. A. Daher, Graduate Student, Department of Wildlife Science, Texas A&M University, College Station, TX 77843, pers. commun. June 1978.

area from which other *Etropus* spp. have not been reported.

Distinguishing Characters

Etropus crossotus larvae have a dashlike melanophore at the base of each pectoral fin. Internal pigment along the dorsal surface of the notochord is extensive. Two elongate dorsal rays are present from preflexion (4.6 mm) through transformation. Caudal vertebrae (25-26, very rarely 24) can be counted by midflexion (5.4 mm). Lateral pigment is relatively heavy. Flexion is complete at 9-10 mm SL. The larval mouth and eye are small. The left pelvic fin has a full complement of six rays. Length at transformation is 10-12 mm. Larvae usually appear in collections from March through August.

Pigmentation

Pigmentation of *E. crossotus* larvae is relatively heavy. Pigment on the gas bladder and on the ventral and dorsal surfaces of the body is the most striking. Most useful for identification is internal pigment along the dorsal surface of the notochord and a melanophore at the base of the pectoral fin.

By about 4.6 mm (Fig. 10A) and throughout larval development, the dorsal one-third of the

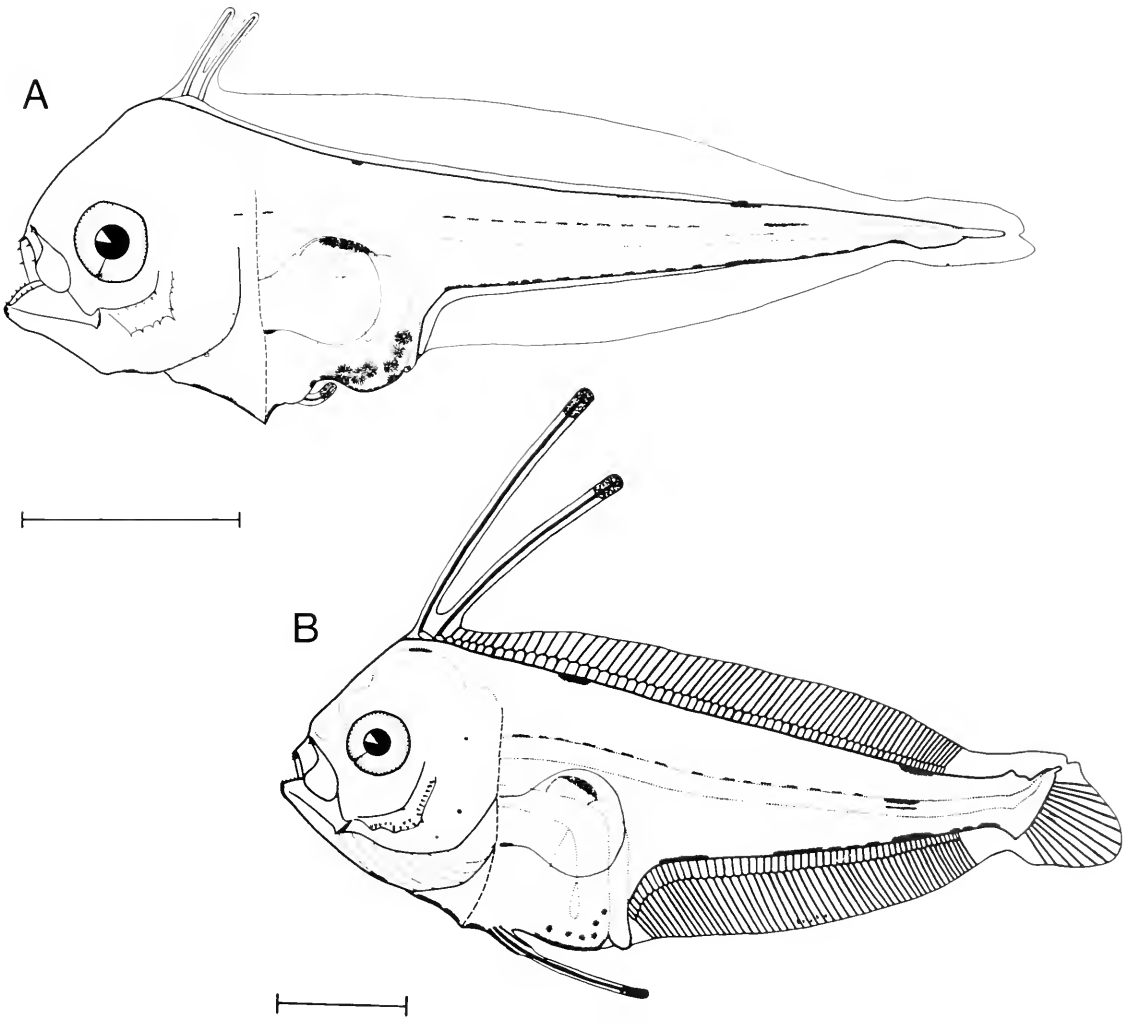


FIGURE 10.—Larval stages of *Etropus crossotus*: A. Preflexion (early caudal formation), 4.6 mm; B. Midflexion, 6.0 mm. Scale = 1 mm.

left side of the gas bladder is fairly heavily pigmented, usually with three or four distinct melanophores. The right side of the gas bladder is similarly pigmented until late flexion. Internal notochordal pigment consists of a series of fine dashes along the dorsal surface and is more extensive then in known *Citharichthys* larvae. Preflexion and early flexion larvae have up to about 12 pigment dashes between the gas bladder and caudal centrum 15. From about caudal centra 15 to 18 (range 14-20) there is a distinct series of heavy dashes which usually form a nearly solid line throughout development. An internal melanophore that appears to be associated with the notochord is located below the hindbrain near the otic capsule, where the notochord joins the brain. Dashlike clusters of pigment develop along the dorsal and ventral body margins between the pectoral fin and the caudal fin base. These clusters have not completely formed in the preflexion specimen, but three dorsal clusters and ventral pigment are present. During preflexion, a melanophore may be present on the ventral edge of the caudal finfold, opposite the midpoint of incipient hypural bones.

Throughout larval development, a continuous or broken line of pigment (the length of three to five centra) is on the lateral midline about two-thirds of the way from the anus to the notochord tip. One or two melanophores are on each side of the symphysis of the lower jaw. The posterior margin of the articular is covered with a stellate melanophore. A stellate melanophore is present at the junction of left and right branchiostegal membranes, just forward of the isthmus. About one to three internal melanophores are present near the pectoral fin base and just forward of the cleithrum beneath the angle of the last gill arch (visible through the opercle). Usually, a melanophore is on the anterodorsal edge of the urohyal. The ventral body margin between the isthmus and pelvic fin is fairly heavily pigmented with a few distinct melanophores or a continuous band of pigment. Several melanophores are present along the ventral and lateral surfaces of the abdomen and sometimes along the hindgut near the anus. The lower edge of both pectoral fin bases is lined with a dashlike melanophore. The second left pelvic ray has melanophores along its distal end. A series of small melanophores is present along the distal tips of anal pterygiophores.

During early flexion (4.9 mm), one, or rarely two, diffuse internal melanophores appear above the hindbrain.

During midflexion (5-6 mm, Fig. 10B), melanophores appear along the distal ends of the elongate dorsal rays. A group of melanophores may be present at the distal ends of the middle anal rays. Melanophores begin appearing at the bases and along the sides of middle caudal rays.

During flexion, internal notochordal pigment increases. Midflexion and late flexion larvae have up to about 5 pigment dashes between the cleithrum and gas bladder and up to about 18 dashes between the gas bladder and caudal centrum 15. From midflexion through postflexion, a small amount of pigment usually is on the anteroventral edge of the maxillary.

By late flexion (6 mm), the gas bladder has become oriented toward the left side, and greater development of musculature obscures the gas bladder from the right side. By about 8.5 mm, musculature begins to obscure notochordal pigment, except for the heavy dashes in the caudal band area. There is no evidence of a melanophore on the opercle; however, one or two small melanophores occasionally appear on the interopercle during late flexion. By about 8.5 mm, concentrations of pigment have formed around the first through third left pelvic rays. Pigment at the distal margin of the right pelvic fin appears at about the same time.

During postflexion (10.5 mm, Fig. 11A), a small melanophore appears on the upper lip. Groups of melanophores are present along the margins of dorsal and anal fins of some specimens.

In the nearly transformed specimen (10.3 mm, Fig. 11B), heavy posterior notochordal pigment is still obvious. Additional internal melanophores have appeared posterior to the hindbrain. Myoseptal pigment is well developed, mostly adjacent to dorsal and anal pigment clusters. As in *Citharichthys* larvae, this forms a caudal band. A midlateral cluster of melanophores is present near the caudal fin. Melanophores have formed along the anterior surface of the head from the snout to the dorsal fin. External and internal melanophores are present along the hindgut. Melanophores have formed along the proximal ends of groups of some dorsal and anal rays.

Morphology (Figs. 10, 11; Tables 3, 8)

General morphological features are similar to those of *Citharichthys cornutus*, with the qualification that the smallest *E. crossotus* specimen examined was 4.6 mm NL. Adult morphomet-

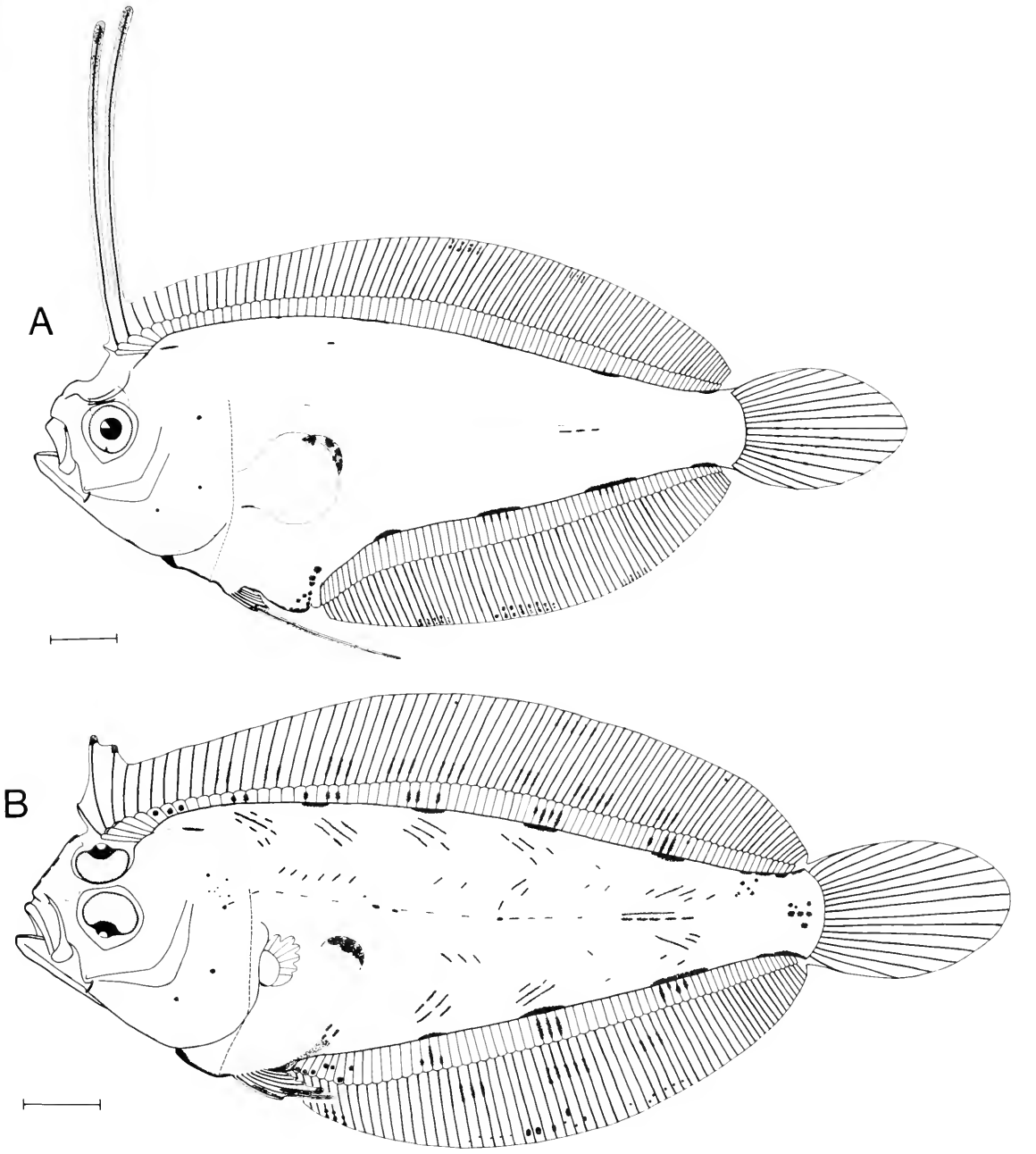


FIGURE 11.—Larval stages of *Etropus crossotus*: A. Transforming, 10.5 mm; B. Nearly transformed, 10.3 mm. Scale = 1 mm.

rics given in the following discussion are from Gutherz (1967).

The larval mouth is relatively small. During flexion and postflexion relative mouth size is similar to that of *C. spilopterus*. The adult mouth is the smallest of known western North Atlantic *Etropus* and *Citharichthys* species. Larval upper jaw length/BL is fairly constant at 7.0-7.2%. Larval upper jaw length/HL decreases from 30% to 27% (preflexion to postflexion). Adult upper jaw length/HL is 21-27%. Larval lower jaw length/BL is fairly constant at 9.6-9.8%. Larval lower

TABLE 8.—Measurements (mm) of larvae and a juvenile of *Etropus crossotus*. Pref = preflexion, ECF = early caudal formation, Early = early flexion, Mid = midflexion, Late = late flexion, Post = postflexion. S = symmetrical, 1 = 0 to one-third of the way to the dorsal ridge, 2 = one-third to two-thirds of the way to the dorsal ridge, 3 = two-thirds to all the way to the dorsal ridge, T = nearly transformed.

Body length	Upper jaw length	Lower jaw length	Snout length	Eye diameter	Head length	Snout to anus length	Total length	Head depth	Body depth at pelvic fin	Body depth at anus	Body depth at third hemal spine	Caudal peduncle depth	Flexion stage	Right eye position
4.6	0.32	0.44	0.24	0.34	1.1	1.8	4.6	1.3	[1]1.2	[1]0.98	[1]0.53		ECF	S
4.9	0.35	0.43	0.27	0.37	1.2	2.1		1.6	1.6	1.4	0.89	0.23	Early	S
5.4	0.38	0.50	0.32	0.39	1.4	2.4	5.6	1.7	1.9	1.7	0.99	0.27	Early	S
5.4	0.43	0.66	0.32	0.41	1.4	2.4	6.0	1.9	2.1	1.9	1.3	0.48	Mid	S
5.5	0.40	0.53	0.40	0.36	1.4	2.5	5.8	1.9	2.0	1.8	1.3	0.43	Mid	S
5.5	0.37	0.52	0.35	0.40	1.5	2.6	6.0	1.9	2.0	1.8	1.2	0.43	Mid	S
5.6	0.43	0.57	0.33	0.40	1.4	2.4	5.9	1.8	2.1	1.9	1.3	0.37	Mid	S
5.7	0.40	0.51	0.33	0.37	1.4	2.4	5.7	1.7	1.9	1.7	1.1	0.31	Mid	S
5.7	0.35	0.49	0.29	0.35	1.4	2.4	6.0	1.8	1.9	1.8	1.2	0.35	Mid	S
5.8	0.34	0.49	0.35	0.38	1.4			1.8	1.9		1.2	0.34	Mid	S
6.0	0.43	0.56	0.40	0.42	1.6	2.7	6.5	2.0	2.2	2.1	1.4	0.43	Mid	S
6.0	0.37	0.51	0.32	0.41	1.5	2.8	6.6	2.0	3.0	1.8	1.3	0.52	Mid	S
6.0	0.50	0.62	0.42	0.43	1.6	2.8	6.8	2.1	2.4	2.2	1.6	0.53	Mid	S
6.1	0.51	0.72	0.37	0.47	1.7	2.6		2.1	2.3	2.3	1.6	0.68	Late	S
6.2	0.41	0.57	0.38	0.41	1.6	3.0	7.2	2.2	2.5	2.4	1.8	0.63	Late	S
6.9	0.50	0.67	0.47	0.46	1.9	3.2	8.2	2.3	2.8	2.6	2.0	0.73	Late	S
7.4	0.54	0.74	0.53	0.49	2.0	3.3	8.8	2.5	3.1	3.0	2.5	0.83	Late	1
8.2	0.49	0.70	0.56	0.50	2.3	3.8	10.1	2.8	3.5	3.7	3.0	1.1	Late	1
8.3	0.53	0.71	0.53	0.54	2.2	3.6	10.1	2.8	3.3	3.5	2.8	1.0	Late	S
8.3	0.63	0.78	0.53	0.54	2.2	3.6	10.1	2.9	3.5	3.8	3.2	1.1	Late	1
8.5	0.69	0.84	0.63	0.58	2.4	3.6	10.8	3.0	3.6	3.7	3.1	1.1	Late	1
9.1	0.70	0.92	0.57	0.61	2.4	3.6	11.4	3.0	3.7	3.9	3.4	1.2	Late	1
9.3	0.73	0.96	0.70	0.67	2.7	3.9		3.4	4.0	4.1	3.5	1.2	Late	1
9.3	0.64	0.84	0.63	0.65	2.6	4.0	11.9	3.4	3.8	4.1	3.6	1.2	Late	1
9.3	0.60	0.86	0.67	0.57	2.4	3.9	11.2	3.0	3.8	4.0	3.4	1.1	Post	1
9.5	0.71	0.90	0.70	0.63	2.6	4.0	11.9	3.3	4.0	4.3	3.7	1.3	Late	2
9.6	0.72	0.96	0.73	0.61	2.6	4.1	11.9	3.4	4.2	4.4	3.9	1.3	Post	1
10.3	0.80	1.1	0.75	0.71	3.0	3.4	12.7	3.3	3.7	3.7	3.7	1.2	Post	T
10.5	0.75	0.99	0.63	0.66	2.7	4.0	12.9	3.5	4.3	4.8	4.0	1.3	Post	2
10.5	0.76	1.1	0.80	0.64	2.8	4.1	12.9	3.5	4.2	4.6	4.0	1.3	Post	3
10.8	0.71	1.0	0.59		2.6	4.1	13.2	3.4	4.3	4.7	4.1	1.4	Post	1

[1]Measurement does not include dorsal or anal pterygiophores.

jaw length/HL decreases greatly from 41% to 36-37%.

The larval snout is moderate but exhibits a relatively fast growth rate. Snout length/BL increases from 5.2% to 6.8%. Snout length/HL increases from 22% to 26%.

The eye is relatively small in larvae and moderate in adults. Larval eye diameter/BL decreases from 7.4% to 6.3%. Larval eye diameter/HL decreases greatly from 32% to 24%. Adult eye diameter/HL is about 22-28%.

The larval head is of moderate length but relatively shallow depth. In adults, the head is the shortest of known western North Atlantic *Etropus* and *Citharichthys* species. Larval head length/BL increases from 23% to 26%. Adult head length/BL is 20-25%. Larval head depth/BL increases from 29% to 33-34% and is similar to that of *C. gymnorhinus*.

Larval snout to anus length is moderate. Snout to anus length/BL increases from 39% (preflexion) to 44% (flexion) and then decreases to 39% (postflexion). This length is similar to that of *C. gymnorhinus* during flexion and postflexion.

Early larvae are relatively shallow, but abdominal and tail depths increase quickly, and as adults, this species and *E. rimosus* are the deepest bodied of known western North Atlantic *Etropus* and *Citharichthys* species. During postflexion, the dorsal and ventral profiles of *E. crossotus* are relatively convex. Larval body depth at pelvic fin/BL increases greatly from 26% to 40%. Larval body depth at anus/BL increases greatly from 21% to 43% and is similar to that of *C. gymnorhinus* during flexion and postflexion. Larval body depth at third hemal spine/BL increases greatly from 12% to 38%. Adult body depth/BL is 50-58%. Larval caudal peduncle depth/BL increases from 9.6% (flexion) to 12.6% postflexion).

Fin and Axial Skeleton Formation

Caudal skeleton development is similar to that of *C. cornutus*. Size ranges of available specimens in each stage are as follows: Early caudal formation, 4.6 mm NL; early flexion, 4.9-5.4 mm NL; midflexion, 5.4-6.0 mm NL; late flexion, 6.1-9.5 mm NL; postflexion, 9.3-10.8 mm SL. Caudal rays become calcified between early flexion (4.9 mm NL) and late flexion (about 6.5 mm NL).

All precaudal neural spines stain with alizarin at 4.6 mm NL. Some caudal neural spines and hemal spines stain with alizarin at 4.6 mm NL, and all do by 5.6 mm NL. All precaudal and caudal centra stain with alizarin at about 6.0 mm NL. The urostyle stains with alizarin at 6.2 mm NL. The smallest specimen in which caudal centra could be counted was 5.4 mm NL (midflexion).

The second and third dorsal rays are elongate and moderately separated at the bases from preflexion (4.6 mm NL) through transformation (about 11 mm SL). During early flexion (4.9 mm NL), rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8.0 mm NL) onward. The first ray and most posterior rays are calcified prior to transformation (by about 9.6 mm SL).

During early flexion (4.9 mm NL), anal rays near the middle of the fin begin to calcify. Calcification proceeds anteriorly and posteriorly. Adult counts are present from late flexion (about 8.0 mm NL) onward. The most posterior rays are calcified during late flexion (about 9.3 mm NL).

Development of the left pelvic fin precedes that of the right. The left pelvic fin bud appears during preflexion (before 4.6 mm NL). Rays develop between early caudal formation (4.6 mm NL) and late flexion (8.5 mm NL). The second ray is the first to appear; it is elongate. The first ray appears soon after the second; it may be slightly elongate. The right pelvic fin bud appears during midflexion (5.5 mm NL). Rays develop between midflexion (5.8 mm NL) and late flexion (8.5 mm NL). Each complete fin has six rays.

Rayless, fanlike, larval pectoral fins are present on the smallest available specimen (4.6 mm NL). Calcification of rays in the left fin occurs during late transformation (10-11 mm SL).

Cephalic Spination

Preopercular spines (Table 4) were present in the smallest preflexion specimen (4.6 mm NL, Fig. 10A). With development (Fig. 10B), additional spines appear until maximum numbers of about 24 on the left (range 18-29) and 22 on the right (range 16-27) are reached during midflexion (5.4-6.0 mm NL). Thereafter, spines are lost until none or only a few remain at transformation (Fig. 11B).

Most specimens had three or four relatively inconspicuous frontal-sphenotic spines on each side, including one or two that were noticeably stronger.

Larval Teeth (Table 5)

The early caudal formation specimen (4.6 mm NL, Fig. 10A) had three upper and five lower teeth on each side. Early flexion larvae (4.9-5.4 mm NL) have three upper and five or six lower teeth on each side. During midflexion (5.4-6.0 mm NL), there are three to five upper and five to seven lower teeth on each side. During late flexion (6.1-9.5 mm NL), larvae usually have four upper and seven lower teeth on each side. During postflexion (9.3-10.8 mm SL), there are usually four or five upper and seven lower teeth on each side. The nearly transformed specimen (10.3 mm SL, Fig. 11B) had seven upper and more than nine lower teeth on each side.

Transformation

Migration of the right eye may begin as early as late flexion (7.4 mm NL) or as late as postflexion (10.8 mm SL). The right eye moves from the right side of the head around the dorsal fin origin (Fig. 11A) as in *C. arctifrons* and *E. microstomus* (Richardson and Joseph 1973). The right eye reaches its final position on the left side of the head at about 10-12 mm SL.

Occurrence

Larvae were collected in the Cape Fear River Estuary during May (pers. obs.) and in the Gulf of Mexico off Louisiana west of the Mississippi River Delta during July and August (Walker[7]). Moe and Martin (1965) suggested a spawning season from March to at least June for the eastern Gulf of Mexico off Florida (based on ripe

[7]H. J. Walker, Research Technician, North Carolina State University, Cape Fear Estuarine Laboratory, P.O. Box 486, Southport, NC 28461, pers. commun. July 1977.

females). Capture of a ripe female from the same area in June was reported by Topp and Hoff (1972). Christmas and Waller (1973) suggested that spawning may be nearly continuous throughout the year. However, that observation was partly based on the occurrence of one juvenile specimen during January and another during February that could have been spawned in the late summer or early fall. Therefore, the season may extend beyond August, but the evidence is not yet complete.

Comparisons

Larval Characters

Morphology seems to be influenced by the environment and duration of larval existence. *Citharichthys cornutus* and *C. gymnorhinus* are found in deeper water and may have longer pelagic larval stages than *C. spilopterus* or *E. crossotus*. In some respects, the latter two species are similar to each other and dissimilar to the first two. *Citharichthys spilopterus* and *E. crossotus* have only two elongate dorsal rays, as opposed to three in the other two species. They have smaller, less conspicuous frontal-sphenotic spines, and fewer larval teeth. (However, the jaws of *C. spilopterus* later grow at a relatively fast rate and acquire correspondingly more adult teeth.) During transformation, the origin of the dorsal fin is slightly farther forward relative to the right eye in *C. cornutus* and *C. gymnorhinus* than in the other two species. (However, after transformation the dorsal origin is more anterior relative to the right eye in all three *Citharichthys* species than in *E. crossotus*.) *Citharichthys spilopterus* and *E. crossotus* larvae have smaller eyes and mouths than the other two. They also complete transformation at a smaller size.

Known similarities among *Citharichthys* larvae that are not shared with *Etropus* larvae include the absence of a pectoral melanophore (except possibly in *C. macrops*), less extensive internal notochordal pigmentation, and, later, more gill rakers. Except for a shallower body and smaller eyes, *C. arctifrons* larvae are morphologically similar to those of *C. cornutus* and *C. gymnorhinus*. *Etropus microstomus* larvae are similar to those of *E. crossotus*.

Larval Occurrence

Differences among distributions of larvae (Append. Table 5) can be helpful in identifying them to species. Months of occurrence of larvae reported here are those in which larvae have been collected throughout the ranges of the respective species (except that data for *C. macrops* are from the southern part of its range, and data for *C. arctifrons* and *C. arenaceus* are from the northern parts of their ranges). Because most sampling was not continuous throughout the year, presence in other months is not precluded; however, enough is known to delineate approximate spawning seasons for most of the species. Larval occurrence of *C. cornutus*, *C. gymnorhinus*, *C. spilopterus*, and *E. crossotus* was discussed in the earlier species' accounts.

Throughout their ranges, *E. microstomus* spawns from March through August and *E. rimosus* spawns from September to April (Leslie 1977). Leslie suggested that spawning of the two species may be temporally distinct. This conflicts with spawning of *E. microstomus* reported from May to December (Richardson and Joseph 1973), and my information is not sufficient to resolve this conflict. However, Scherer and Bourne (1980) collected *E. microstomus* eggs in September and larvae in October in Block Island Sound, which is north of the reported adult range (Table 1). In the eastern Gulf of Mexico, larvae of *E. rimosus* smaller than 4 mm NL were common in November, January, February, and May (Dowd 1978).

Small juveniles (≥13 mm SL) of *C. abbotti* were caught in the Gulf of Mexico from Veracruz to Campeche, Mexico, in June and September (Dawson 1969), indicating a spawning season approximately from May through August, or longer.

Citharichthys macrops larvae smaller than 4 mm NL were caught in the eastern gulf in May and November (Dowd 1978). Topp and Hoff (1972) reported juveniles from the same part of the gulf during the fall and winter. The season probably extends from May through November, and possibly longer.

Richardson and Joseph (1973) reported a spawning season approximately from May to December for *C. arctifrons* in the Chesapeake Bight, with peak spawning from July through October.

Dawson (1969) reported a 27 mm SL specimen of *C. arenaceus* caught in the British West Indies in November. This may indicate summer spawning, probably during August or September at least.

Citharichthys amblybregmatus and *C. dinoceros* are deepwater forms. Because of the constancy of their environment, they may have extended spawning seasons, but little is known of their habits.

Considering the geographic and bathymetric distributions of adults (Table 1) and probable spawning periods (Append. Table 5), it is unlikely that large numbers of larvae of different species of western North Atlantic *Citharichthys* and *Etropus* cooccur in the ichthyoplankton at any given time. Among the six deepwater species, *C. amblybregmatus* and *C. dinoceros* larvae probably occur relatively far from shore. Apparently, there is little difference between larval occurrence of *C. gymnorhinus* and *C. cornutus*, but spawning centers or peak periods could be distinct. Topp and Hoff (1972) suggested that adults of the two species were bathymetrically separated, *C. gymnorhinus* being found in shallower water. *Etropus rimosus* adults occur in shallow water and do not spawn during the summer. *Citharichthys arctifrons* has a more northern distribution than the preceding three species and its spawning peak is in the summer, probably earlier than that of *E. rimosus*. Among the three coastal species, the geographic range of *C. arenaceus* is distinct from those of the other two, and *C. macrops* and *E. microstomus* cooccur only off the Carolinas. In this area of overlap, *C. macrops* probably spawns in the fall and *E. microstomus* in the spring. Among the three estuarine and coastal species, *C. abbotti* spawns in the warmer months and may be restricted to very shallow water. *Citharichthys spilopterus* spawns in the colder months, beginning in late summer in the Gulf of Mexico and in mid to late fall off the Carolinas. *Etropus crossotus* may spawn from March through the summer, or later, in the gulf, but probably does not begin off the Carolinas until after most spawning activity of *C. spilopterus* is finished.

SUMMARY

The caudal fin formula (4-5-4-4) is the most reliable character for linking larval specimens to the group of paralichthyine genera *Citharichthys*, *Cyclopsetta*, *Etropus*, and *Syacium*.

The most useful characters for identification to genus are number of elongate dorsal rays, degree of cephalic spination, and pigmentation. Known western North Atlantic *Syacium* and *Cyclopsetta* larvae have 5-10 elongate dorsal rays and well-developed preopercular and frontal-sphenotic spines. Known western North Atlantic *Citharichthys* larvae have two or three elongate dorsal rays, small (or no) preopercular spines, small frontal-sphenotic spines, no pectoral melanophore (except possibly *C. macrops*), little notochordal pigmentation, usually large eyes and mouths, and (except for *C. arctifrons*) high gill raker counts. Known western North Atlantic *Etropus* larvae have no or two elongate dorsal rays, small preopercular and frontal-sphenotic spines, a melanophore at the base of the pectoral fin, extensive notochordal pigmentation, small eyes, and low gill raker counts.

Table 9 summarizes the most useful characters for distinguishing larvae of the six species of western North Atlantic *Citharichthys* and *Etropus* that have been described in detail. The best characters for determining species are number of elongate dorsal rays, number of caudal vertebrae, pectoral and notochordal pigmentation, number of left pelvic rays (*C. gymnorhinus*), head shape and snout to anus length (*C. spilopterus*), number of gill rakers, and length at transformation.

Citharichthys arctifrons larvae have three elongate dorsal rays, no preopercular spines, many caudal vertebrae, a small eye, large mouth, and few gill rakers. *Citharichthys cornutus* larvae have three elongate dorsal rays, a strong first left pelvic ray, heavy pigmentation, a large eye and mouth, and relatively many gill rakers. *Citharichthys gymnorhinus* larvae have three elongate dorsal rays, few caudal vertebrae, five left pelvic rays (with the first weak), a distinct caudal pigment band, large eye and mouth, and relatively many gill rakers. *Citharichthys spilopterus* larvae have two elongate dorsal rays, few caudal vertebrae, little pigmentation, a small eye and mouth, very blunt anterior profile, short snout to anus length, and relatively many gill rakers.

Etropus crossotus larvae have two elongate dorsal rays, heavy pigmentation, a small eye and mouth, and many (for the genus) gill rakers. *Etropus microstomus* larvae have no elongate dorsal rays, a small eye, and few gill rakers.

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TABLE 9.—The most useful characters, in order of ontogenetic appearance, for distinguishing larvae of four species of *Citharichthys* and two species of *Etropus*.

Character	*C. arctifrons*[1]	*C. cornutus*	*C. gymnorhinus*	*C. spilopterus*	*E. crossotus*	*E. microstomus*[1]
Pectoral melanophore (before transformation)	Absent	Absent	Absent	Absent	Present	Present
Notochordal pigment (before transformation)	Caudal only	Caudal only	Caudal only	Caudal only	From brain to caudal area	From brain to caudal area
Elongate dorsal rays (before transformation)	3	3	3	2	2	0
Caudal vertebrae	26-28	25-26	23-24	[2]23-24(25)	[2](24)25-26	[2]24-25(26)
Lateral pigment (before transformation)	Moderate	Heavy	Moderate	Light	Heavy	Moderate
Length at flexion (mm)	9	9-10	7-8	7-8	9-10	7
Left pelvic rays (full complement)	6	6	5	6	6	6
Left preopercular spines (during preflexion-flexion-postflexion)	0	14-31-22	17-22-31	31-31-16	17-20-11	Several
Eye diameter/BL in % (during preflexion-flexion-postflexion)	7	10-10- 8	9- 9- 9	10- 8- 7	7- 7- 6	7
Upper jaw length/BL in % (during preflexion-flexion-postflexion)	10	10-11-10	10- 9- 9	10- 7- 7	7- 7- 7	9
Lower jaw length/BL in % (during preflexion-flexion-postflexion)		13-14-13	12-13-13	12-10- 9	10-10-10	
Snout to anus length/BL in % (during preflexion-flexion-postflexion)	42	46-46-39	43-44-40	40-39-32	39-44-39	40
Gill rakers on the lower limb of the first arch (at transformation)	6- 8	10-15	9-14	9-15	6- 9	4- 7
Length at transformation (mm)	13-15	~18	~18	9-11	10-12	10-12
Snout spine (at about transformation)	May be present	Present (in males?)	Present (in males?)	Absent	Absent	Absent
Symphyseal spine (after transformation)	Absent	Present (in males?)	Present (in males?)	Absent	Absent	Absent

[1]Data for *C. arctifrons* and *E. microstomus* are mostly from Richardson and Joseph (1973)
[2]Uncommon counts given in parentheses

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APPENDIX TABLE 1.—Frequency distributions of caudal vertebral counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	21	22	23	24	25	26	27	28	29	*N*	$\bar{X}$
C. abbotti	19	96	9							124	21.92
C. arenaceus	3	38	8							49	22.10
C. gymnorhinus			9	27						36	23.75
C. spilopterus			23	109	8					140	23.89
E. rimosus			3	50	53	5				111	24.54
E. microstomus				51	61	2				114	24.57
C. macrops				27	46					73	24.63
E. crossotus				1	69	15				85	25.16
C. cornutus					15	29				44	25.66
C. amblybregmatus					5	16				21	25.76
C. arctifrons						5	34	3		42	26.95
C. dinoceros						([2])			([2])		

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Leslie 1977; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *E. microstomus* and *C. arctifrons*); and original data for larvae, juveniles, and adults of *C. gymnorhinus*, *C. spilopterus*, *C. macrops*, *E. crossotus*, and *C. cornutus*.
[2]Extremes of counts.

APPENDIX TABLE 2.—Frequency distributions of anal fin ray counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	48	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	76	*N*	$\bar{X}$
C. arenaceus	([2])		1	11	8	14	9	3																	46	53.6
E. microstomus		([2])	1	1	2	8	14	22	32	31	23	15	6	5	([2])										160	57.5
C. gymnorhinus			2		4	3	3	9	13	6	10	3	2												55	56.8
C. abbotti				1	5	13	37	35	22	14	4	1													132	55.9
E. rimosus					1	5	5	17	25	42	57	57	38	41	16	6	1								311	59.5
C. spilopterus							([2])	15	24	30	41	26	11	4	([2])										151	58.6
C. macrops								1	1	6	2	5	17	16	13	12									73	61.6
E. crossotus										1	1	1	6	10	12	13	13	3		([2])					60	63.2
C. arctifrons										([2])		1	1	7	6	10	23	16	8	6	2	2	1		83	65.3
C. cornutus											([2])	3	2	7	4	6	3	1	1						27	63.0
C. amblybregmatus															1	3	2	3	1	9		1	2		22	67.0
C. dinoceros																						([2])		([2])		

[1]Compiled from Gutherz 1967, Dawson 1969, Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *C. arctifrons*); and original data for juveniles and adults of *C. gymnorhinus*, *C. spilopterus*, *C. macrops*, *E. crossotus*, and *C. cornutus*.
[2]Extremes of counts, not included in totals.

APPENDIX TABLE 3.—Frequency distributions of dorsal fin ray counts for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	67	68	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	90	95	*N*	$\bar{X}$
E. microstomus	([2])	2	1	2	7	8	22	21	26	24	23	12	6	4	1	1	([2])						160	76.1
C. arenaceus		([2])	1	2	11	10	9	7	3	2													45	73.5
C. gymnorhinus			7	8	12	9	8	5	3	1													53	72.7
E. rimosus			2		8	16	18	43	57	52	48	40	17	4	4	1							310	76.7
C. abbotti					1	5	13	23	30	23	23	11	2	1									132	76.4
C. spilopterus						1	4	4	14	35	32	24	26	11	5	1		1					158	78.3
C. cornutus							1	1	1	3	5	8	6	5	1	1	1						33	79.2
C. macrops							1	1	1	1		3	9	10	12	12	11	8	3				72	82.1
C. arctifrons								1	1	3	8	8	14	14	17	7	2	3	3	2			83	81.0
E. crossotus								([2])	3	2	8	12	10	11	8	6			1	([2])			61	80.1
C. amblybregmatus											2	3	1	2	6	3	2	1	2				22	81.9
C. dinoceros																					([2])	([2])		

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970; Topp and Hoff 1972; Leslie 1977; Sopher, T. R., a meristic and morphometric study of geographic populations of *Etropus microstomus*. Unpubl. manuscr., 5 p., Virginia Institute of Marine Science, Gloucester Point, VA 23062; S. L. Richardson, Research Assistant Professor, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. December 1976 (unpubl. data for *C. arctifrons*); and original data for juveniles and adults of *C. gymnorhinus*, *C. spilopterus*, *C. cornutus*, *C. macrops*, and *E. crossotus*.
[2]Extremes of counts, not included in totals.

APPENDIX TABLE 4.—Ranges of number of gill rakers on the lower limb of the first arch for western North Atlantic species of *Citharichthys* and *Etropus*.[1]

Species	Range	Species	Range
E. rimosus	3-7	*C. spilopterus*	9-15
E. microstomus	4-7	*C. cornutus*	10-15
C. arctifrons	6-8	*C. arenaceus*	12-15
E. crossotus	6-9	*C. macrops*	12-16
C. dinoceros	7-10	*C. abbotti*	13-16
C. gymnorhinus	9-14	*C. amblybregmatus*	18-24

[1]Compiled from Gutherz 1967; Dawson 1969; Gutherz and Blackman 1970, and Topp and Hoff 1972.

APPENDIX TABLE 5.—Probable spawning seasons of seven species of *Citharichthys* and three species of *Etropus*.[1] Estuarine = usually found in estuaries and shallow coastal waters < 40 m; Shallow = usually found in shallow coastal waters < 40 m, rarely in estuaries; Intermediate = usually found at 30-140 m depths, rarely shallower; Deep = usually found deeper than 140 m, seldom shallower.

Species	Jan.	Feb	Mar.	Apr	May	June	July	Aug.	Sept	Oct	Nov	Dec.	Adults occur	Larvae occur
C. gymnorhinus	×	×	×	×	×	×	×	×		×	×		Intermediate	Offshore
C. cornutus	·	·	·	·	·	·	·	·		·	×		Deep	Offshore
E. crossotus			·	·	·	·	·	·					Estuarine	Offshore and in estuaries
E. microstomus			×	×	·	·	·	·	·				Shallow	Offshore
C. abbotti					+	+	+	+					Estuarine	?
C. macrops					×	+	+	+	+		×		Shallow	Offshore
C. arctifrons					·	×	·	·	·	·	×	×	Intermediate (and Deep)	Offshore
C. arenaceus									+				Shallow	?
C. spilopterus	×	×	×	·					·	·	×	×	Estuarine	Offshore and in estuaries
E. rimosus	·	·	×	×	·				·	·	·	×	Intermediate	Offshore
C. amblybregmatus						?							Deep	Offshore?
C. dinoceros						?							Deep	Offshore?

[1]Compiled from Dawson 1969; Topp and Hoff 1972; Richardson and Joseph 1973; Leslie 1977; Dowd 1978; Scherer and Bourne 1980, and unpublished data from collections of South Carolina Marine Resources Research Institute, Louisiana State University, North Carolina State University, and Texas A&M University. × = times based on collections of larvae and ripe females, + = times based on collections of juveniles.

AVOIDANCE OF TOWED NETS BY THE EUPHAUSIID *NEMATOSCELIS MEGALOPS* [1]

P. H. WIEBE,[2] S. H. BOYD,[2] B. M. DAVIS,[2] AND J. L. COX[3]

ABSTRACT

Avoidance of towed nets by the common oceanic euphausiid crustacean *Nematoscelis megalops* was studied by comparing aspects of its sampling distribution as revealed by day and night catches of two nets of different size, one with a 1 m^2 mouth opening and one with a 10 m^2 opening. Both nets yield essentially the same pattern in vertical distribution. Paired tows yield a highly significant agreement in nighttime abundance estimates, but do not give comparable daytime estimates. Night catches, especially with the smaller net, exceed day catches, an effect which is interpreted as resulting from greater avoidance during the day. Comparisons between nets show that neither size net has a superior catch rate, day or night. No particular size group of the species is caught with greater efficiency by either net. When *N. megalops*' center of distribution is shallower, differences between day and night catches can be substantially enhanced.

Application of Barkley's avoidance theory indicates that the potential advantage of greater mouth area of the larger net is effectively cancelled by individuals reacting to the approach of the net at a greater distance. Other theoretical predictions which depend upon the assumption of increasing escape velocities as a function of body size are not corroborated by the field data. Thus, field population size-frequency distributions are probably not materially affected by avoidance.

The evidence suggests that *N. megalops* uses vision to detect the net approach. Net contrast with the background due to down-welling light during the day and bioluminescence produced in and around the net both day and night appear to be the most likely stimuli. Future efforts to reduce net avoidance by species like *N. megalops* must focus on reduction of these signals.

Avoidance of capture by towed nets is a major source of underestimation bias associated with zooplankton abundance measurements (Clutter and Anraku 1968; Wiebe and Holland 1968; Wiebe 1971). This factor is perhaps the most important determinant of the accuracy of abundance estimates for some of the larger zooplankton species. Patchiness of zooplankton may cause large differences between successive tows taken at a single station (Wiebe 1971; Wiebe et al. 1973), but the error induced by this factor is not comparable with avoidance error, since patchiness "error" is essentially unbiased. The precision of the estimate of abundance for a particular station location will improve with greater sample numbers, but avoidance error will persist as an underestimation bias. Since patchiness of zooplankton exists on scales from the microscale (centimeters to meters) to the mesoscale (hundreds of kilometers) (Mackas and Boyd 1979; Haury et al. 1978), patchiness itself can be viewed not as a sampling problem, but rather as a reflection of natural distributions. Avoidance and technical problems such as clogging and escapement (Vannucci 1968) represent sampling biases which tend to obscure our picture of these natural distributions. Although clogging and escapement are still important sources of error, improved net design can, in many instances, eliminate these as major problems (Smith et al. 1968). Zooplankton avoidance of nets, at least for some species, remains as an important sampling problem.

Avoidance is variable, depending upon such factors as time of day; light regime; size, shape, and color of the net; speed of tow; species; sex or developmental stage of the organisms; their physiological state; and absolute density (Fleminger and Clutter 1965; Isaacs 1965; McGowan and Fraundorf 1966; Brinton 1967; Clutter and Anraku 1968; Laval 1974; Boyd et al. 1978). Almost certainly this diversity of factors is one of the major reasons for a lack of consensus regarding the extent or magnitude of avoidance bias for

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any particular zooplankton group. Further, the mechanisms by which an oncoming net is detected and avoided are not well known (Clutter and Anraku 1968).

Theoretical studies of avoidance (Barkley 1964, 1972; Clutter and Anraku 1968; Murphy and Clutter 1972; Laval 1974) have drawn attention to important behavioral aspects of avoidance and how these behavioral features are likely to interact with net size and towing speed. Avoidance theory provides a framework for the design of avoidance field studies and the interpretation of their results, as Barkley's (1972) examples clearly demonstrated. We have applied avoidance models to data on the euphausiid *Nematoscelis megalops* to determine its response to different net types under different conditions. Since our data on this relatively abundant species indicated substantial avoidance effects, we have examined it in some detail.

In studies of *N. megalops* vertical distributions (Wiebe and Boyd 1978; Boyd et al. 1978) night tows were consistently observed to produce higher numerical density estimates than tows at the same station during the day. These tows were taken with a multiple net system with a 1 m^2 mouth opening (MOCNESS, Wiebe et al. 1976). Although horizontal patchiness may have contributed in an unbiased way to the day/night differences in catch rate, the overall comparison of day and night tows strongly suggested greater avoidance during the day. Unfortunately, there were too few day/night pairs at a single station to demonstrate this by pairwise comparison.

During 1976 and 1977, as part of a multidisciplinary study of Gulf Stream cold core rings (Lai and Richardson 1977; Richardson 1980), more complete observations of day/night vertical distributions were made at stations in Slope Water and cold core rings. Tows were taken with a 1 m^2 MOCNESS and with a 10 m^2 MOCNESS. As will be demonstrated below, both net systems catch *N. megalops* without apparent size discrimination between the two. Both net systems are avoided to a certain extent, based on day/night catch ratios, but some revealing differences are evident. Using data from both sizes of nets, it is possible to apply Barkley's (1972) avoidance model to obtain independent estimates of the parameters of reaction distance and percent capture within a certain animal size range, and through a comparative analysis reach some tentative conclusions regarding avoidance mechanisms in the species studied.

METHODS

The combinations of 1 m^2 and 10 m^2 MOCNESS tows were taken at nine stations (Fig. 1), with additional information about each tow in Table 1. Stations 1-4 were sampled in April 1977 on RV *Knorr* cruise 65 and stations 5-9 were sampled on *Knorr* 71. Station 1 was in cold core ring "Bob," a 2-mo old ring; station 2 in ring "Al," a 6-mo old ring; station 6 in "Emerson," a relatively old ring; stations 7 and 8 in "Franklin," a middle-aged ring. The other stations were located in the Slope Water. For some comparisons data collected with the 1 m^2 MOCNESS on earlier cruises will be used; information about these tows (those noted in Table 2) is reported by Ortner et al. (1978). Station positions for the remaining tows are given in Table 1.

At the majority of stations day and night tows were taken with both the 1 m^2 and 10 m^2 MOCNESSes. The 1 m^2 net was equipped with nine nets of 333 μm nylon mesh netting dyed dark blue and was fished obliquely so that eight strata were sampled. Generally, the strata sampled were 1,000-850, 850-700, 700-550, 550-400, 400-300, 300-200, 200-100, 100-0 m; usually between 600 and 1,000 m^3 were filtered in each strata. Occasionally in the Slope Water when sharp hydrographic gradients were present, the sampling intervals were modified to bracket the physical discontinuities.

The 10 m^2 MOCNESS is a scaled up version of the 1 m^2 net system described by Wiebe et al. (1976). On the tows reported here, it was equipped with five nets of 3 mm nylon mesh white netting. This net system was fished obliquely with four of the five nets sampling 250 m intervals from 1,000 to the surface. Each net filtered between 13,000 and 43,000 m^3. As with the 1 m^2 MOCNESS, the first net is fished while lowering the system to the maximum depth of the tow to provide uniform drag and to prevent kiting of the system at the start of the stratified oblique haul. Neither system has a bridle in front of the nets.

The nets of both systems are opened and closed with commands sent via conducting cable from a surface deck unit. For both systems on *Knorr* 65, we used an underwater unit which measures and telemeters to the surface depth temperature, conductivity, angle of the net system from the vertical, flow past the net, and information regarding the electrical and mechanical function of the opening/closing mechanism. The trans-

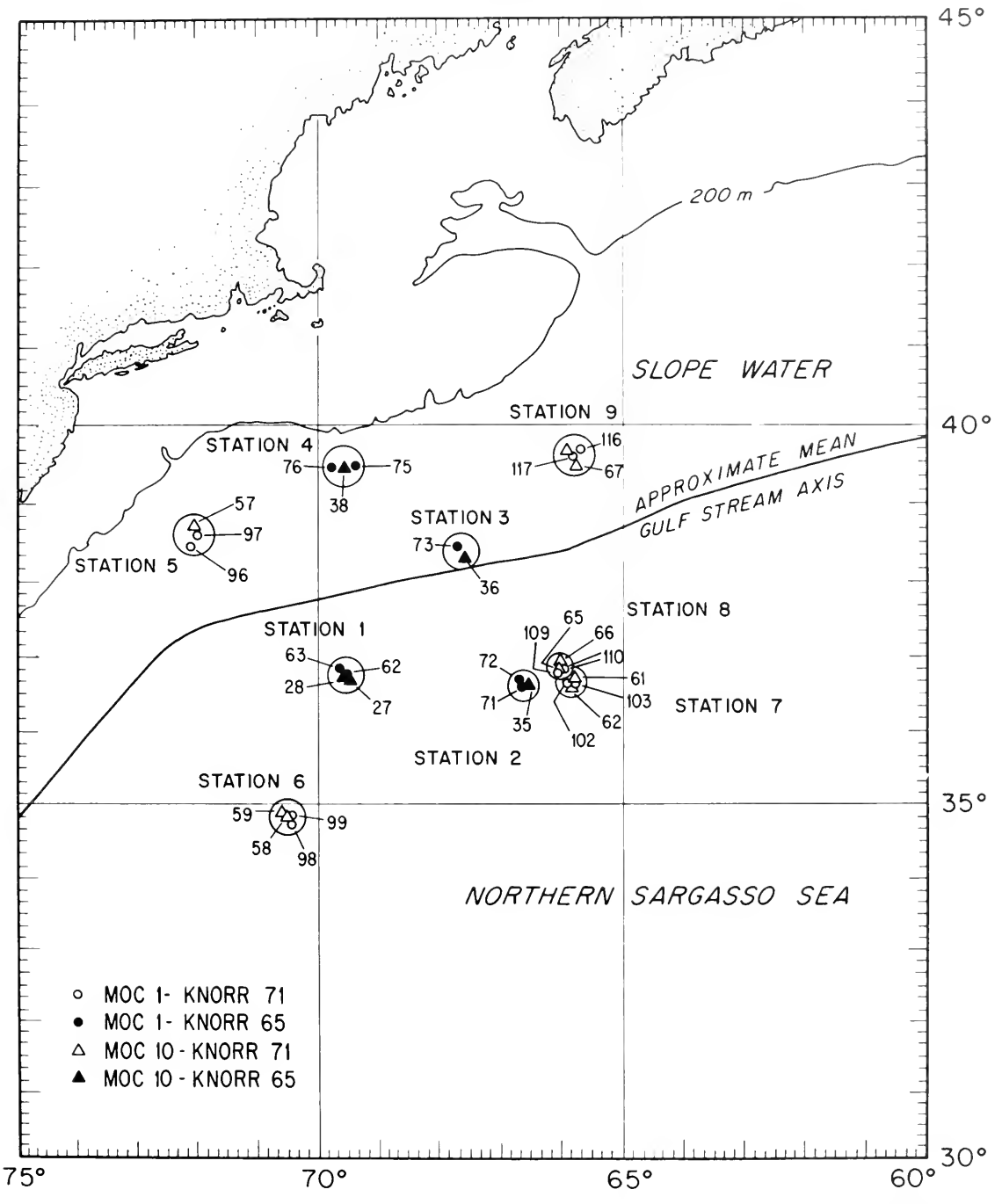

FIGURE 1.—Position of the 1 m^2 and 10 m^2 MOCNESS tows within each of the nine station areas (indicated by large open circles). Small solid triangles and circles are night tows; open ones are for day tows. Each tow listed in Table 1 is designated by its tow number.

TABLE 1.—Summary of tow statistical information for the 1 m^2 and 10 m^2 MOCNESS (MOC-1, MOC-10) tows taken in 1977 at the nine station locations illustrated in Figure 1. D = Day; N = Night.

Cruise no.	Station no	MOC 1	Longitude W	Latitude N	Time of tow	MOC 10	Longitude W	Latitude N	Time of tow	Date of tow	MOC 1/MOC 10 10° isotherm depth (m)
Knorr 65	1	62 D	69°30.1' 69°30.8'	36°43.2' 36°47.8'	1019- 1228	27 D	69°30.0' 69°25.9'	36°46.5' 36°38.6'	1352- 1744	4/17	300/330
		63 N	69°33.0' 69°34.8'	36°49.0' 36°53.2'	0115- 0335	28 N	69°30.0' 69°27.2'	36°41.1' 36°49.0'	2055- 0030	4/17-18	296/270
	2	72 D	66°39.0' 66°38.8'	36°38.0' 36°35.6'	0910- 1128	35 D	66°36.9' 66°34.4'	36°35.6' 36°31.3'	1303- 1650	4/24	717/690
		71 N	66°39.6' 66°39.0'	36°30.5' 36°36.2'	2100- 2322					4/23	
	3	73 D	67°42.4' 67°37.5'	38°19.3' 38°21.3'	0955- 1128	36 D	67°37.0' 67°37.4'	38°21.3' 38°11.7'	1248- 1639	4/28	234/290
	4	76 D	69°41.3' 69°38.0'	39°24.0' 39°28.0'	0705- 0913					4/30	
		75 N	69°26.6' 69°31.9'	39°28.5' 39°25.1'	2107- 2314	38 N	69°31.0' 69°43.0'	39°24.6' 39°21.1'	2345- 0345	4/29-30	200/255
Knorr 71	5	96 D	72°03.0' 72°00.0'	38°25.9' 38°29.9'	0930- 1204					10/23	
		97 N	71°54.5' 71°52.1'	38°36.8' 38°40.6'	2201- 0015	57 N	71°54.1' 71°51.0'	38°39.9' 38°47.0'	0052- 0050	10/23-24	190/190
	6	98 N	70°20.2' 70°21.5'	34°46.5' 34°50.2'	2150- 0005	58 N	70°21.9' 70°16.0'	34°50.8' 34°52.0'	0201- 0501	10/28-29	545/550
	7	102 D	65°52.1' 65°47.0'	36°40.1' 36°42.3'	0471- 1104	61 D	65°46.9' 65°40.0'	36°43.0' 36°46.0'	1345- 1652	11/3	309/340
		103 N	65°53.5' 65°47.9'	36°40.0' 36°42.5'	2243- 0059	62 N	65°48.9' 65°40.0'	36°42.2' 36°48.0'	0123- 0502	11/3-4	360/330
	8	109 D	66°00.0' 66°00.8'	36°44.1' 36°49.1'	0910- 1138	65 D	65°58.3' 65°46.0'	36°49.0' 36°52.0'	1232- 1646	11/6	310/375
		110 N	65°57.8' 65°59.5'	36°49.8' 36°55.1'	1901- 2123	66 N	65°58.8' 66°10.0'	36°56.0' 37°05.0'	2140- 0213	11/6-7	278-290
	9	117 D	65°51.1' 65°51.2'	39°32.9' 39°38.8'	1117- 1359	67 D	65°42.1' 65°48.0'	39°26.0' 39°33.0'	1308- 1628	11/15	200/230
		116 N	65°47.0' 65°45.6'	39°35.0' 39°40.6'	1933- 2156	68 N	65°49.0' 65°51.0'	39°36.8' 39°35.0'	0026- 0500	11/15-16	232/205

mitted data were recorded on magnetic tape. They were also processed by a shipboard computer (Hewlett-Packard[4] 2100) and plots of depth versus temperature and salinity were produced. On *Knorr* 71, the 10 m^2 net was deployed with a simplified electronics package which did not have a conductivity sensor and which transmitted data at a slower rate. For this latter system, plots of depth versus temperature and angle of the net were made with a Hewlett-Packard X, Y, Y recorder. During all of these tows, net speed, as indicated by the flowmeter, was closely monitored and adjustments to the ship speed and/or winch speed were made to keep the net moving ahead at 2±0.5 kn (3.71±93 km/h). All samples were preserved in 5-10% Formalin buffered to pH 8.0 with sodium borate.

For 162 of the 190 samples resulting from the tows listed in Table 1, we sorted and counted the entire sample for adult and adolescent (without adult sexual characteristics) *N. megalops*. Very large catches were split with a Folsom plankton splitter (McEwen et al. 1954) and between one-half and one thirty-second of the sample was counted. Wet weights were determined either on all or a sizable fraction of the sorted individuals. Battered or disfigured individuals were excluded from this analysis. Individuals were blotted on absorbent paper and then weighed to ±0.1 mg on a Cahn model 7500 digital top-loader millibalance. Total body length (tip of rostrum to tip of telson) was determined on a small subset of individuals from both the *Knorr* 65 and 71 collections in order to establish a relationship between wet weight and length (Fig. 2) for subsequent calculations of potential escape velocity based on body length. The geometric mean regression equation (Ricker 1973) which was fit to these data is similar to those presented by Mauchline (1967) for a variety of euphausiid species.

In some comparisons of the sampling capabilities of the two MOCNESSes and in the application of Barkley's (1972) avoidance theory, we have used the average numbers per 1,000 m^3 for

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

TABLE 2.—The ratio (Night/Day) of night 1 m^2 and 10 m^2 MOCNESS catch of *Nematoscelis megalops* (no./m^2) divided by the paired day catch at stations in the Slope Water and cold core rings and the depth where the cumulated frequency of occurrence equals 50% in the night tow. Information about the tows taken on *Chain* 125 and *Knorr* 53 is given in Ortner et al. (1978).

Tow and cruise	Station or area	MOCNESS tow no. (night/day)	Night/Day[1]	Depth of 50% (m)
1 m^2 MOCNESS				
Knorr 65	Station 1	63/62	5 6	82
	Station 2	71/72	33 0	80
	Station 4	75/76	1 5	340
Knorr 71	Station 5	97/96	5 9	345
	Station 6	98/99	1 7	500
	Station 7	103/102	29 0	370
	Station 8	110/109	1 3	325
	Station 9	116/117	33.0	150
Chain 125	Slope Water	[1]20/21	63.4	220
	Slope Water	[1]19/18	10.9	260
	Ring "D"	[1]5/8	([2])	300
Knorr 53	Slope Water	35/37	48 9	280
	Slope Water	41/42	.57	380
	Slope Water	39/40	([2])	450
	Ring "D"	[1]29/27	2.7	650
	Ring "D"	[1]33/31	6.4	450
Knorr 62	Slope Water	57/58	1 5	245
	Ring "AI"	45/47	2.6	505
10 m^2 MOCNESS				
Knorr 65	Station 1	28/27	3.67	130
Knorr 71	Station 6	58/59	2.66	700
	Station 7	62/61	0 68 (1 47)	375
	Station 8	66/65	0.84 (1.19)	370
	Station 9	68/67	2 93	180

[1]Vertical distribution of *N. megalops* on these tows illustrated in figure 5 of Wiebe and Boyd (1978).
[2]None present in day collection.

the water column. These values were obtained by combining the stratified oblique hauls to form a composite tow. Note that because the water column sampled is 1,000 m, the integrated number per 1,000 m^3 for the column is identical to numbers per square meter.

RESULTS

Analysis of 1 m^2 and 10 m^2 MOCNESS Observations

The vertical distribution of *N. megalops* at stations where pairs of 1 m^2 and 10 m^2 MOCNESS tows were taken (Fig. 3) illustrates the large variations in depth distribution that can occur in the different hydrographic regimes and at different times of year. As previously described by Wiebe and Boyd (1978), this species generally has its center of distribution above 300 m in Slope Water. Exceptions in Slope Water are associated with the presence of warm core rings. In young cold core rings such as "Bob," the center of distribution is also shallow. In most of the older rings we have sampled, the distribution of *N. megalops* deepens as is evident in "Franklin" and "Emerson" (see also figure 5 in Wiebe and Boyde 1978).

Very close agreement between the two net systems in the shape of the vertical distribution is found, especially at night (Fig. 3). The night 1 m^2 and 10 m^2 MOCNESS tows also show significant agreement in the integrated numbers caught per square meter ($r = 0.99$; $P<0.05$). In contrast, the paired day tow data are considerably more variable and do not show significant agreement in integrated numbers per square meter ($r = 0.13$; $P>0.05$).

Clearest evidence for differential day/night net avoidance by *N. megalops* is found in the catch data obtained by the 1 m^2 MOCNESS (Fig. 3). Without exception, for each of the eight day/night pairs of tows taken on *Knorr* 65 and *Knorr* 71, the day estimate of numbers per square

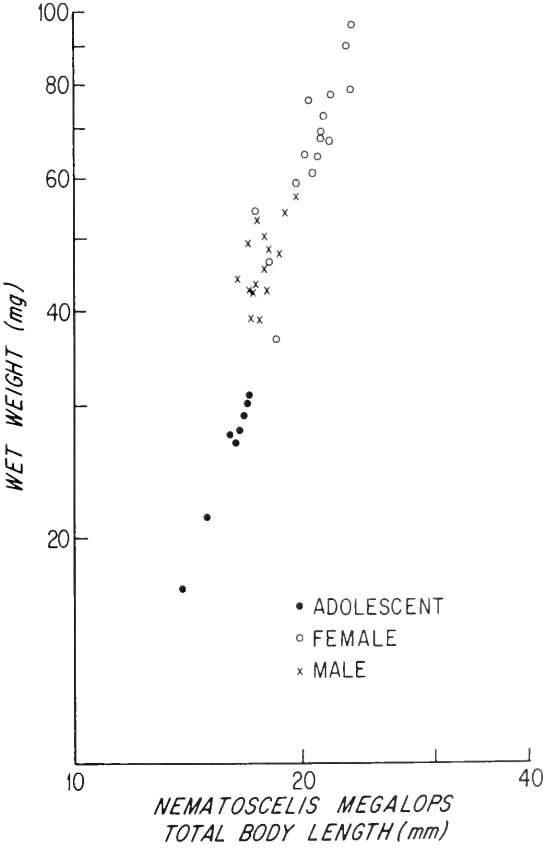

FIGURE 2.—Relationship between total body length, carapace length, and wet weight of *Nematoscelis megalops*.

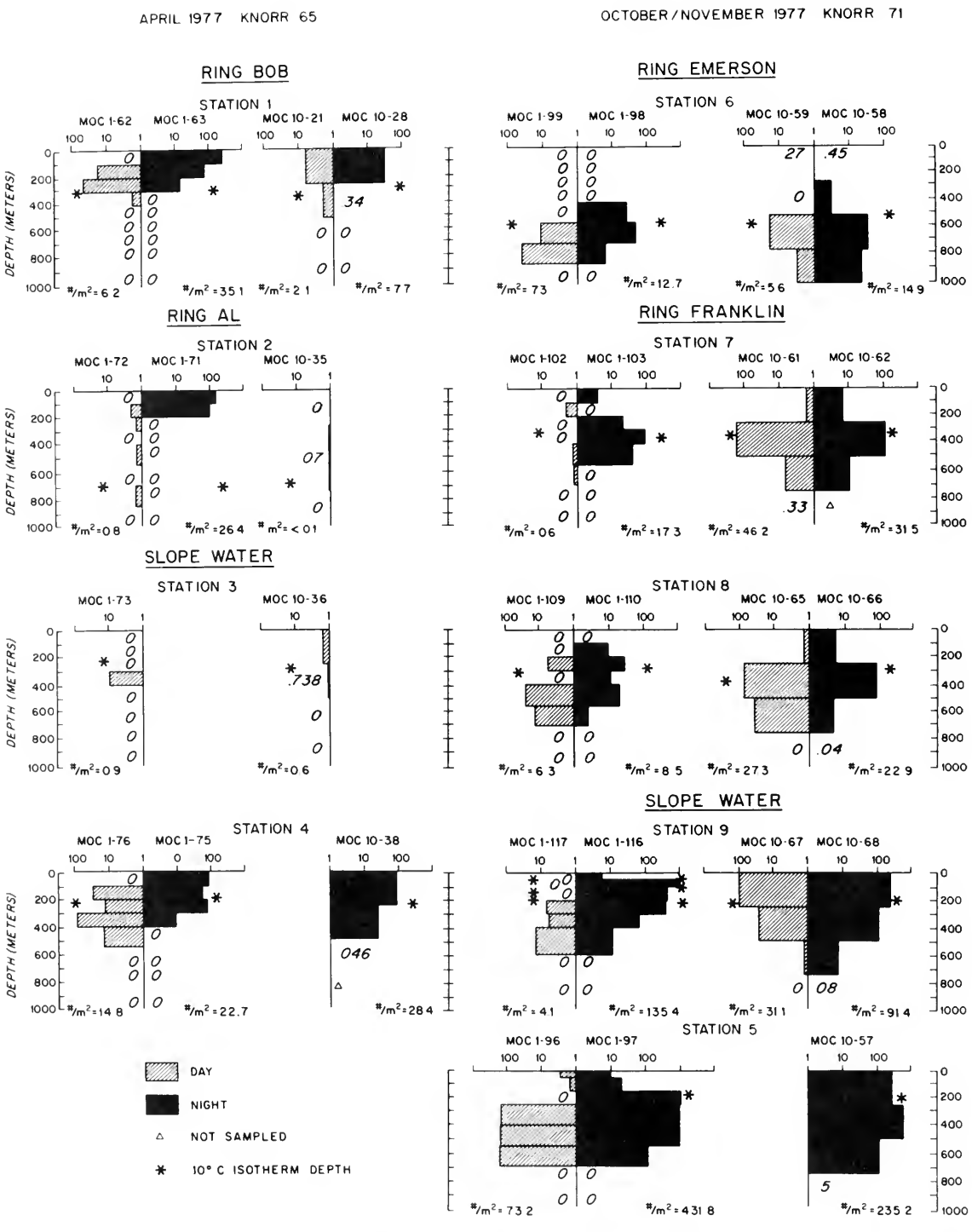

FIGURE 3.—Vertical distribution of *Nematoscelis megalops* in the Slope Water and in variously aged cold core rings based on collections made with the 1 m² and 10 m² MOCNESSes on two cruises taken 6 mo apart. Night samples are blacked; day samples are crosshatched.

meter for the water column is less than the corresponding night catch. In every case, sampling extended below the maximum depth of occurrence of the population and there is no evidence that any individuals of the population migrated vertically out of the depth zone sampled during the day. Therefore, it is highly significant that all of the day values were less than the respective night ones ($P<0.005$). This result gains importance if we also consider 10 other day/night pairs of 1 m^2 MOCNESS tows in which *N. megalops* was collected on previous cruises (*Chain* 125, *Knorr* 53, *Knorr* 62). For nine of these pairs, moderately to dramatically higher catches in the night tow were obtained (Table 2). The single exception to this pattern was a pair of Slope Water tows taken near the continental shelf in the wake region of a warm core ring (tows 41, 42). But these two tows were displaced in space by several miles, and the night tow was taken nearer the warm core ring where a lower catch might have been expected.

Of the 18 day/night pairs of 1 m^2 MOCNESS tows, 17 yield higher density estimates at night. Patchiness in the distribution of *N. megalops* contributed to variability to these estimates but as an unbiased variance component, it does not affect our expectation that one-half of the day and one-half of the night tows in day/night pairs should be the larger. Thus it is unlikely that patchiness of this species is responsible for the significantly higher night catches that we have observed ($P<0.001$). We know of no other explanation than avoidance to explain this result.

There are only five pairs of 10 m^2 MOCNESS observations of the vertical distribution of *N. megalops*. For two of these, the integrated day catch is larger than the corresponding night catch and, therefore, night catches are not significantly larger than day catches ($P>0.05$). This result either means that there is no day/night differential avoidance of the 10 m^2 net or that in the face of other sources of error such as patchiness, we have too few day/night pairs of observations to observe the avoidance effect. If avoidance were affecting only the smaller net then at least we would expect that the 1 m^2 net day catches per unit volume would be consistently smaller than the corresponding 10 m^2 net day catches. We might also expect that night catches with the 1 m^2 net would be smaller than the 10 m^2 net. Neither comparison yields a significant result ($P>0.05$; day MOCNESS 1 tows greater than day MOCNESS 10 tows in four out of seven comparisons; night MOCNESS 1 tows greater than night MOCNESS 10 tows in three out of seven comparisons). Thus within the limits of error, by day or by night both net systems provide comparable estimates of the number of *N. megalops* living in the water column at a given station.

It is possible that the lack of differences in the catching rates between the two nets is due to the different mesh sizes. Small individuals might have been caught more efficiently by the 1 m^2 net while larger individuals could have avoided this net better and conversely for the 10 m^2 net except that small individuals would have been lost due to escapement through the mesh. The size-frequency data in Figures 4 and 5 do not support this possibility. While there is considerable variability between net tow pairs, in terms of absolute abundance, neither net system systematically catches large or small individual *N. megalops* in the size range counted better than the other. A similar observation can be made if comparisons are made on the relative abundances in a given size class (Fig. 6).

There is one other potentially significant trend in the data that is important to note. The magnitude of the day/night avoidance does not appear to be uniform with depth. For the 1 m^2 MOCNESS, largest differences between paired night and day catches where both are positive occur when the center of distribution of *N. megalops* is above 300-400 m and minimum differences occur at or below these depths (Table 2). Linear regression of the ratio of night to day catch (N/D) versus depth of the center of the distribution at night (50% of occurrence with depth) is significant at $P = 0.1$. There is a similar pattern in the 10 m^2 MOCNESS tows, although as mentioned above, the day/night differences in catching rates are considerably smaller.

In summary, there is clear evidence for differential day/night avoidance of the 1 m^2 MOCNESS. Furthermore, there are no significant differences in the size range of adolescent or adult *N. megalops* caught by the 1 m^2 or 10 m^2 MOCNESS systems nor in either system's estimates of its abundance in the water column at a given station when day or night pairs are compared. Although differences between pairs of day/night catches for the 10 m^2 MOCNESS are statistically not significant, the entire data set when considered as a whole strongly suggests that *N. megalops* is also avoiding the 10 m^2 net, albeit to a lesser extent.

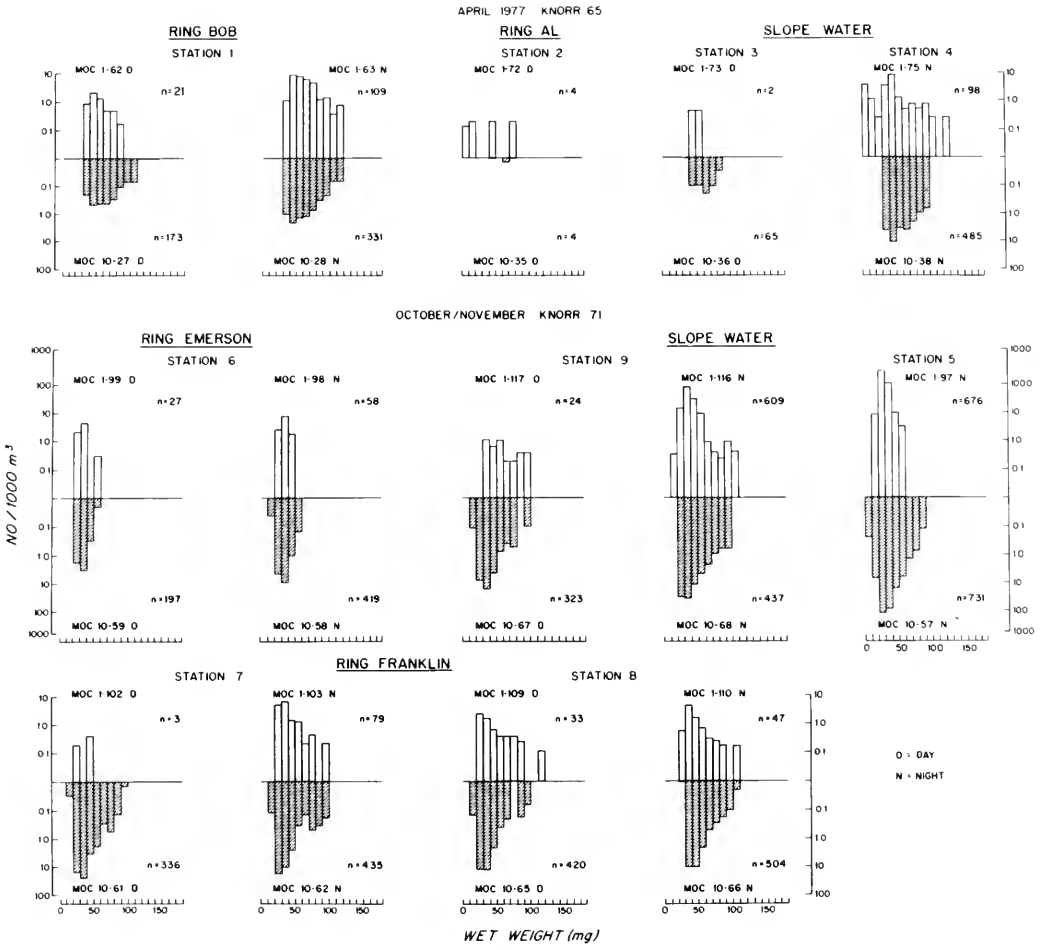

FIGURE 4.—Comparison of the composite size-frequency distribution (expressed as No./1,000 m^3 for a given wet weight interval) of *Nematoscelis megalops* caught by the MOCNESS 1 (shaded) and the MOCNESS 10 (crosshatched) for tows taken on the same day or night. n = the number of individuals used to construct the histogram.

Application of Barkley Avoidance Theory

Since it is likely that *N. megalops* avoids both net systems, it must detect the approach of either net at some distance in front of the net, resulting in a response which permits a certain percentage of the population to avoid capture. Determination of the avoidance percentage and reaction distance requires an indirect approach, since no other means are available. The theoretical framework on the process of net avoidance developed by Barkley (1964, 1972) provides a means for estimating these parameters according to a quantitative theoretical model. Barkley (1972) formulated the problem in the following way:

$$\text{Catch} = (\text{volume sampled}) \times (\text{no. of organisms unit volume}) \times (\text{probability of capture}) - (\text{losses}) \quad (1)$$

"Losses" refers to individuals which are enclosed by the net but escape through the net meshes. For the size range of individuals which constitute our "catch," the "losses" term is essentially zero. Since the volume of water sampled has been rather carefully measured, the "probability of capture" (Pc) is of greatest concern. Pc is related to the mean reaction distance (x_0), the radius of the net mouth (R), the net's speed (U), and the organism's mean escape speed (u_e) by the equa-

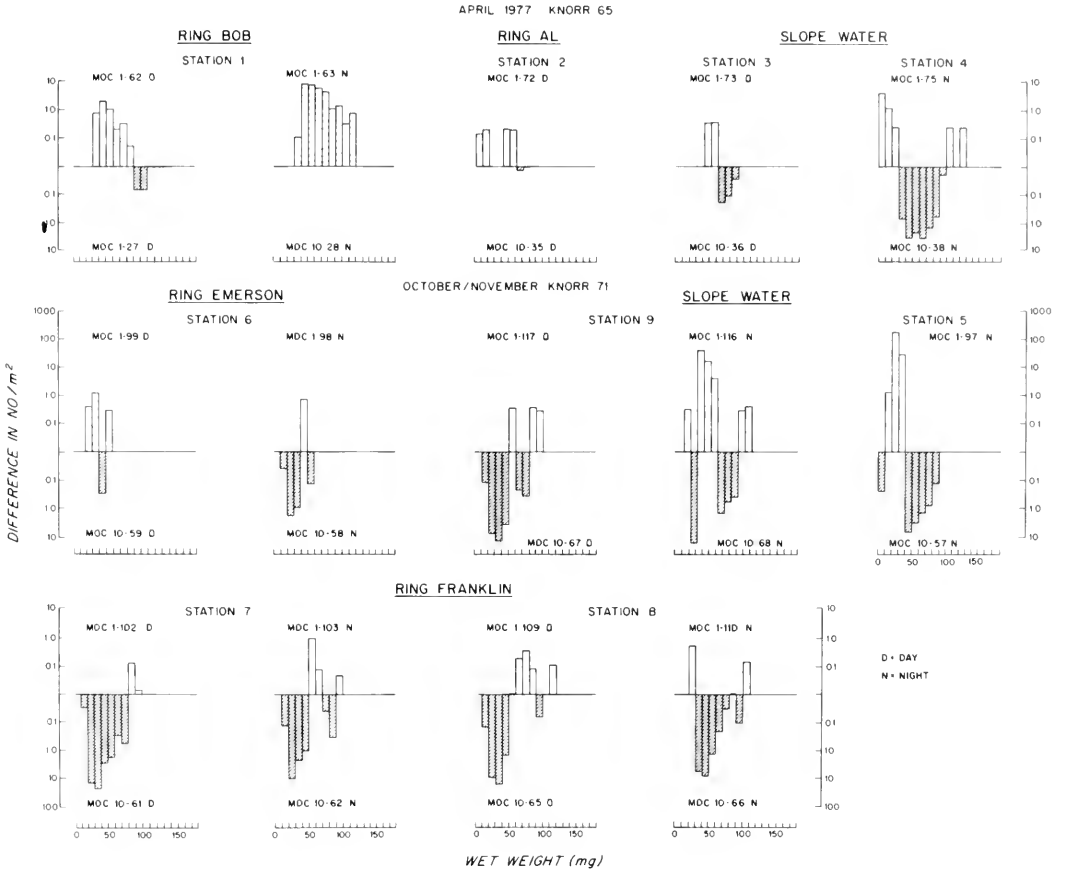

FIGURE 5.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 catches in No./1,000 m^3 for a given wet weight interval. For shaded columns above the line, the MOCNESS 1 catch is greater than the MOCNESS 10 catch and vice versa for crosshatched columns below the line.

tion derived by Barkley (1972, equation 6) wherein:

$$Pc = \left(1 - \frac{x_0\, u_e}{R(U^2 - u_e^2)^{1/2}}\right)^2. \qquad (2)$$

This expression assumes that as the net moves forward through the water, an individual senses the oncoming net and at a distance x_0 in front of the net begins a swimming response in a direction away from the net which is optimal for avoidance. Thus, this equation provides an estimate of the minimum probability of capture.

As a first step in applying these equations to our data, we may recall that for both the paired night tows and the paired day tows differences between the two net systems were not significant, i.e.,

$$\frac{10\ \text{m}^2\ \text{MOCNESS catch}}{\text{volume sampled}} \cong \frac{1\ \text{m}^2\ \text{MOCNESS catch}}{\text{volume sampled}}.$$

If we assume that the number of organisms per unit volume was a constant during the time each pair of tows was taken, then:

$$10\ \text{m}^2\ \text{MOCNESS}\ P_c = 1\ \text{m}^2\ \text{MOCNESS}\ P_c$$

and

$$\left(1 - \frac{x_{10} u_e}{150(100^2 - u_e^2)^{1/2}}\right)^2 = \left(1 - \frac{x_1 u_e}{50(100^2 - u_e^2)^{1/2}}\right)^2$$

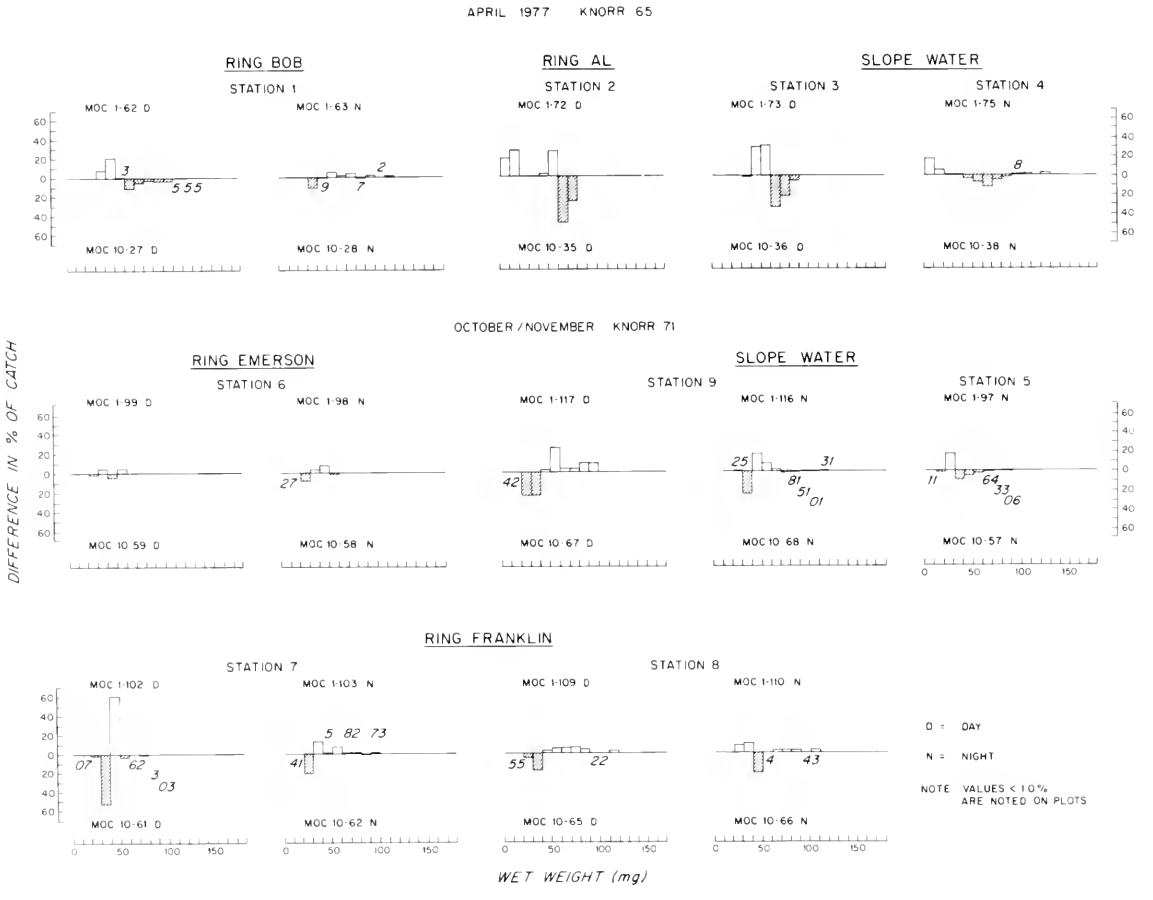

FIGURE 6.—Comparison of the difference between paired MOCNESS 1 and MOCNESS 10 tows in the percent of the catch in a given wet weight interval.

where x_{10} and x_1 refer to the reaction distance for the 10 m^2 and 1 m^2 net systems, where we have approximated the radius of the large net as 150 cm and the small net as 50 cm, and where both nets were towed at approximately 100 cm/s. We are also assuming that the mean swimming speed of the individuals (u_r) is the same for both nets. Solving for the ratio of the reaction distances we find:

$$\frac{x_{10}}{x_1} = 3.0.$$

That is, in order for the two net systems to provide numbers of *N. megalops* per volume filtered which are approximately the same, the reaction distance for the 10 m^2 MOCNESS must be three times greater than for the 1 m^2 MOCNESS.

Since we do not know the absolute abundance of *N. megalops* independent of our net tow estimates for any sampling period, we cannot directly estimate the absolute magnitude of the reaction distance or the minimum probability of capture for either net. It is possible to derive those estimates by a method described by Barkley (1972:808) which involves making a best fit of theoretically derived curves which relate P_c, u_r/U, and X_0/R to observations of u_r/U and the catch/volume filtered for each size class of individuals caught by the nets. In order to make these comparisons, we must have an estimate of the mean escape velocity of an individual (u_r) in a given size class, and ultimately we must make some assumption about population structure, i.e., abundance versus size class of the population sampled.

To make estimates of u_e, we have followed Barkley (1972) and used generalized swimming speed-body length relationships because there is no direct information about u_e for *N. megalops*. However, as discussed below, inconsistencies between model expectations and the field data develop when this assumption is applied. Our basic size-frequency data are in units of wet weight. However, as noted under "Methods," a subset of individuals of *N. megalops* from MOCNESS 10 tows were used to establish the relationship between wet weight and body length (Fig. 2). Mean body wet weight of individuals in each size class was converted to body length (L) and then to relative escape speeds (u_e/U) assuming initially that $u_e = 10\ L$. This assumption is supported by work of Kils (1979) and Semenov (1969). Relative escape speeds were plotted versus the catch/1,000 m^3 in each size class on semilog graph paper scaled so that each plot could overlay a reproduction of the upper panel of Barkley's figure 3 (1972:805). These plots were adjusted vertically to obtain a "best" fit with the x_0/R curves such that a maximum number of points fell between any two of the x_0/R curves (Fig. 7). This produces an estimate of x_0 if it is assumed that the shape of the size-frequency distribution is entirely produced by improvement of avoidance capability with increasing size.

Estimates of reaction distance (x_0) for each net system (Table 3) are between 1.7 and 2.3 for the 1 m^2 MOCNESS and between 4.9 and 6.6 m for the 10 m^2 MOCNESS. No significant differences between night x_0's and day x_0's for either net system are observable. Our initial conclusion was that this was an unreasonable result since intuitively one would expect an increased night catch to be related to reduced nighttime x_0 values

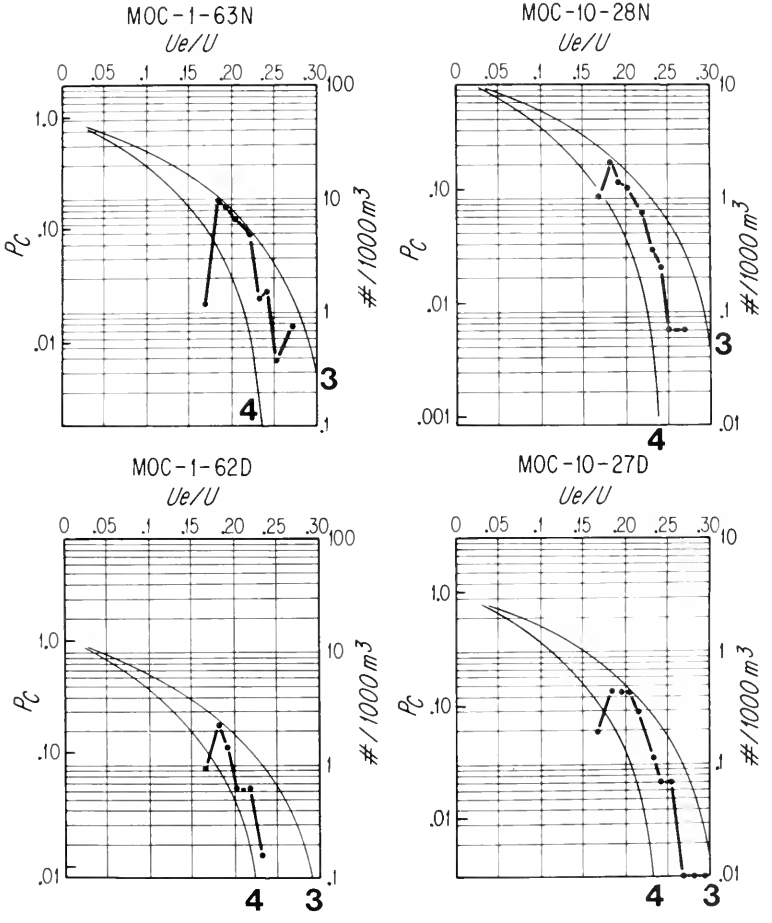

FIGURE 7.—Examples of relative escape speed of *Nematoscelis megalops* individuals versus the catch per 1,000 m^3. Superimposed on this plot are the theoretically derived curves of x_0/R as a function P_c and u_e/U adjusted to give a "best" fit of the observed points.

if individual escape speeds remained constant. However, further analysis reveals that the difference in x_0 for a given day/night catch differential could be a function of the relationship between the observed night catch and the true water column abundance. This is clearly evident if we express the ratio of the day catch per volume sampled (DC) and night catch per volume sampled (NC) in terms of real abundance (A) and percent capture as expressed in Equation (2):

$$\frac{DC}{NC} = A\left(1 - \frac{x_D}{R\sqrt{\frac{U^2}{u_D^2} - 1}}\right)^2 \Bigg/ A\left(1 - \frac{x_N}{R\sqrt{\frac{U^2}{u_N^2} - 1}}\right)^2. \quad (3)$$

If we assume that the daytime escape speed, u_D, is equal to the nighttime speed, u_N, and solve for the ratio of the daytime reaction distance, x_D, to the nighttime reaction distance, x_N, we have:

$$x_D/x_N = \left(\frac{DC}{NC}\right)^{1/2} + \frac{1}{1 - \left(\frac{NC}{A}\right)^{1/2}} - \frac{\left(\frac{DC}{NC}\right)^{1/2}}{1 - \left(\frac{NC}{A}\right)^{1/2}}. \quad (4)$$

We have evaluated this equation assuming a true abundance of 100 individuals per volume, nighttime catches of 99, 90, 10, 1, and 0.1 individuals per volume, and daytime catches of 50, 10 and 1% of the nighttime catch. The ratios of x_D/x_N, plotted as a function of the ratio of NC/A Fig. 8a), shows that only very small differences in reaction distance between day and night are required to explain large day/night catch differentials when the night catch is 10% or less of the true water column abundance. The fact that we see no significant difference in day/night reaction distances suggests our nighttime catches also could be affected strongly by avoidance, and that even at night we have significantly underestimated the numbers of *N. megalops* in the water column.

It could be argued that the day/night catch differential is due to differences in escape speed of the individuals rather than a change in their reaction distance. To explore this we have also solved Equation (3) for the ratio of day escape speed, u_D, to night escape speed, u_N, after assuming $x_D = x_N$.

$$u_D/u_N = \left[\frac{\left[\left(\frac{DC}{A}\right)^{1/2} - 1\right]^2 * \left[\left(\frac{NC}{A}\right)^{1/2} - 1\right]^2 + \left[\left(\frac{DC}{A}\right)^{1/2} - 1\right]^2 * \left[\frac{X_n}{R}\right]^2}{\left[\left(\frac{DC}{A}\right)^{1/2} - 1\right]^2 * \left[\left(\frac{NC}{A}\right)^{1/2} - 1\right]^2}\right]^{1/2}. \quad (5)$$

Note that the ratio of day/night escape speeds is a function of x_N and R as well as DC, NC, and A. The escape speed and radius of net were not in Equation (4) for the ratio of day/night reaction distances. We have evaluated this ratio using the same values noted above. With these results (Fig. 8b), we reach a conclusion similar to that for reaction distance, namely, if reaction distance remains constant between day and night, then small differences in escape speed can explain the day/night catch differential when the night catch is 10% or less of the true abundance.

There is, however, an entirely different explanation which may account for this outcome in application of Barkley avoidance theory to our data. In fitting these data to Barkley's plots of percent capture versus the ratio of x_0/R, two assumptions were required: 1) that all changes in size frequency are due to avoidance and 2) that swimming speed is a function of body size. The second assumption can be examined if one has day/night pairs of tows taken at the same station location with the same size of net. With swimming speed a function of size, Barkley's model

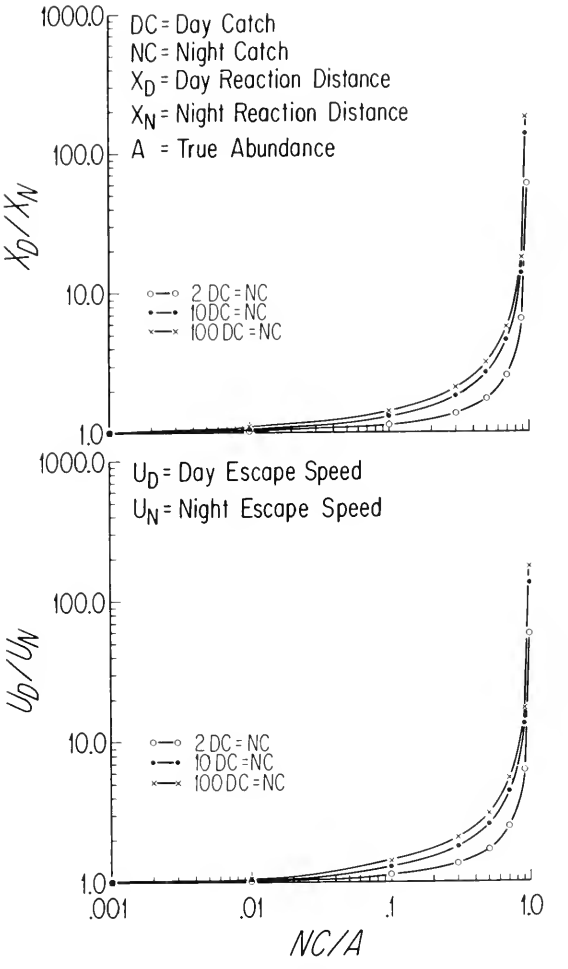

FIGURE 8.—Relationships between the ratio of night catch to true abundance (NC/A) and a) the ratio of day and night reaction distances (x_D/x_N), and b) the ratio of day and night escape speeds (u_D/u_N).

TABLE 3.—*Nematoscelis megalops* reaction distances (x_0) for the 1 m² and 10 m² MOCNESS nets derived from the plots like those in Figure 7.

Station	Cruise	Tow	Day/Night	x_0/R	x_0
1	*Knorr* 65	M-1-62	D	3.4	1.7
		M-10-27		3.3	5.0
		M-1-63	N	3.4	1.7
		M-10-28		3.4	5.0
3	*Knorr* 65	M-1-73	D	3.4	1.7
		M-10-36		(1)	(1)
4	*Knorr* 65	M-1-75	N	(1)	(1)
		M-10-38		3.4	5.0
5	*Knorr* 71	M-1-97	N	4.5	2.3
		M-10-57		4.4	6.6
6	*Knorr* 71	M-1-99	D	4.5	2.3
		M-10-59		4.4	6.5
		M-1-98	N	4.5	2.3
		M-10-58		4.4	6.6
7	*Knorr* 71	M-1-102	D	4.4	2.2
		M-10-61		(1)	(1)
		M-1-103	N	4.4	2.2
		M-10-62		4.4	6.6
8	*Knorr* 71	M-1-109	D	3.5	1.8
		M-10-65		4.4	6.6
		M-1-110	N	4.3	2.2
		M-10-66		4.3	6.4
9	*Knorr* 71	M-1-117	D	3.5	1.8
		M-10-67		4.4	6.6
		M-1-116	N	4.4	2.2
		M-10-68		4.3	6.5

[1]Not sufficient points to derive an estimate; Station 2 omitted for this reason.

TABLE 4.—The ratio of night catch to day catch as a function of individual swimming speed (u_e) as predicted by Barkley's avoidance model (inverse of Equation 3). u_e is assumed to be a function of body size as described in the text.

Body wet weight (mg)	u_e (cm/s)	Night catch[1]	Day catch[1]	Ratio
20	15.08	0.294	0.217	1.35
30	16.32	0.253	0.177	1.43
40	17.56	0.216	0.141	1.53
50	18.80	0.181	0.108	1.66
60	20.04	0.149	0.080	1.84
70	21.28	0.120	0.056	2.12
80	22.52	0.093	0.036	2.57
90	23.76	0.070	0.020	3.42
100	25.00	0.050	0.009	5.47
110	26.24	0.033	0.002	14.57
120	27.48	0.022	0.000	—

[1]Catch units are proportion of individuals present per unit volume

predicts that the ratio of the number of individuals caught per size class at night (NC) to those caught during the day (DC) will increase with increasing individual size (the inverse of Equation 3).

This relationship is illustrated in Table 4 where u_N and u_D are assumed to be equal and 10 body lengths/s, $x_D = 175$ cm, $x_N = 150$ cm, $R = 50$ cm, and $U = 100$ cm/s. This ratio increases dramatically with individual size until at the largest size, the model predicts all individuals avoid capture. No such pattern emerges if we compute the ratio NC/DC for each size class in our paired day/night MOCNESS 1 or MOCNESS 10 tows (Table 5). Thus, the assumption of increasing swimming speed with increasing size does not appear to be valid, i.e., for the size range of individuals used in this study, avoidance swimming speeds are essentially the same. One implication of this finding is that the size-frequency distributions evident in the field data may not be seriously biased by the avoidance although the estimates of average density clearly are.

TABLE 5.—Ratios of night to day catches (number per square meter) of *Nematoscelis megalops* as a function of size for stations where both the MOCNESS 1 and the MOCNESS 10 were taken. ∞ indicates only the night tow caught individuals in the given size class; 0 indicates the opposite patterns.

Body wet weight (mg)	MOCNESS 1—tow no.:					MOCNESS 10—tow no.:				
	117/116	62/63	99/98	102/103	109/110	27/28	59/58	61/62	65/66	67/68
10	∞	—	—	—	—	—	∞	4.4	0	0
20	∞	—	1.2	33.3	0.3	—	2.4	1.1	<0.1	4.0
30	66.6	1.3	1.7	∞	2.6	5.9	2.6	0.4	0.8	2.2
40	45.5	4.0	∞	3.7	2.6	4.8	3.6	0.8	4.8	2.9
50	7.9	5.6	0	∞	1.9	3.6	7.7	0.2	5.6	5.9
60	4.6	1.1	—	∞	0.8	3.2	—	0.5	2.8	5.9
70	2.1	7.7	—	∞	0.7	2.6	—	0.9	∞	1.8
80	0.6	7.7	—	—	0.7	2.9	—	2.5	1.0	∞
90	2.4	∞	—	∞	—	3.5	—	12.5	1.7	6.3
100	∞	∞	—	—	∞	1.0	—	—	∞	—
110	—	∞	—	—	0	7.1	—	—	—	—
120	—	—	—	—	—	0	—	—	—	—
130	—	—	—	—	—	0	—	—	—	—

DISCUSSION

From this application of the Barkley avoidance theory, it appears that estimates of *N. megalops* water column abundance could be substantially underestimated by both nets, even at night. Minimum probabilities of capture derived from best fits to model expectations are 0.1 or less for night catches and 0.01 or less for day catches. However, the fact that we cannot demonstrate a dependence of the ratio of night to day catches on the size of individuals caught strongly suggests the size dependent swimming speed assumption required to apply the model is not valid for this species, a result which is apparently supported by Kils's (1979) data for *Euphausia superba* escape swimming (tail swimming). Being unable to make this assumption means that the field population size-frequency distribution which was observed is probably not materially affected by avoidance. Undeniably some fraction of the *N. megalops* population is avoiding the net systems, and the problem is serious enough to merit an effort to reduce this bias, i.e., to prevent the avoidance from taking place.

The usual strategies suggested to reduce net avoidance, increasing net speed or net size, have serious shortcomings in this case. Our evidence strongly implies that *N. megalops*' response to increased net size is to increase its reaction distance so that the catch rate remains relatively constant. Barkley (1972) reached the same conclusion in a comparison of 1 m diameter net and 3 m IKMT (Isaacs-Kidd midwater trawl) catching rates of the northern anchovy, *Engraulis mordax*. It is possible that by going to still larger nets (i.e., >10 m^2 mouth areas), a reduction in the bias could be effected. However, larger nets would be impractical, if not impossible, to handle on most oceanographic vessels.

As Barkley (1964) has demonstrated, increased net speed is not a feasible strategy for avoidance reduction since increasing the towing speed of a net requires a compensatory reduction in net size. The practical limits to increasing the tow speed are reached at 2 to 3 kn, because of unavoidably extreme wire angles and inordinate amounts of wire required to fish even at moderate depths (to 1,000 m). High speed tows generally result in damaged specimens, reducing their value in studies requiring taxonomic identification or in physiological and biochemical measurements. Finally, as speed of net is increased, the effects of escapement through the meshes is enhanced.

Another means of reducing avoidance, that of camouflaging the net to reduce an animal's ability to detect its presence and thereby reducing the avoidance reaction distance, has been discussed briefly by Clutter and Anraku (1968). There is evidence that it may be an effective strategy for species such as *N. megalops* (LeBrasseur and McAllister, unpublished data cited by Clutter and Anraku 1968). To use this approach, one must first know what kind of a signal the animal is using to detect the oncoming net. Camouflaging the net can be accomplished by reducing the signal until it becomes part of the background (omnidirectional noise). Alternatively, the noise level could be increased until the signal is no longer detectable.

Signals emanating from a net and towing cable include deformation of flow, near field (displacement dominant) or far field (pressure dominant) sound, and light (bioluminescence) (Clutter and Anraku 1968). The importance of

these different signals obviously depends upon the net structure and towing cable configuration and upon the ability of *N. megalops* to sense the various signals. Although there is no direct experimental information about *N. megalops'* sensory capabilities or about the signals being generated by MOCNESS, it seems clear that the primary avoidance stimulus involves day to night variations in light. *Nematoscelis megalops* must use vision to detect the net and can better avoid the net during the day than at night because during the day the net is better illuminated. A fundamental link between the amount of light present and the magnitude of the avoidance is provided by our observation that as individuals live deeper in the water column under substantially reduced daytime light levels, day/night differences in catch rates decline.

But if we accept the results gained by the application of Barkley's model which indicate substantial avoidance takes place at night in the absence of bright sunlight, then other factors must also be important. We propose that bioluminescence is the principal signal and that vision remains the principal means of detection.

Three lines of evidence support the importance of bioluminescence as an avoidance cue. First, in an experiment conducted in the early 1960's, Boden (1969) equipped an IKMT with light meters so that he could monitor the amount of light produced above, below, in front of, and inside the trawl as it was towed at night. Bioluminescent light above the trawl was less than below the trawl but both were considerably lower than that ahead of or in the net. Light within the net was so bright that it recorded off scale and individual flashes were often too numerous to be recorded as such. Light ahead of the net was also exceedingly bright. Boden (1969) speculated that the light ahead of the net was caused by organisms flashing either in response to the light within the net or to pressure or sound waves propagating forward from the net. Second, Neshyba's (1967) experiments with a submarine photometer and strobe light showed that mesopelagic and epipelagic organisms could be stimulated to produce significant amounts of bioluminescence (10^{-4} $\mu W/cm^2$) for a sustained period by proper strobe light flashing. In the absence of artificial flashing, he observed a much lower level of irregular flashing (10^{-8}-10^{-7} $\mu W/cm^2$) similar to that reported by Kampa and Boden (1956), Clarke and Backus (1964), and Boden et al. (1965). Third, it is known that the eyes of euphausiids and decapod shrimps living at midwater depths during the day (i.e., 200-600 m) are sensitive to light levels (10^{-7} to possibly 10^{-9} $\mu W/cm^2$, Clarke 1970) significantly lower than that produced as a result of bioluminescence.

These lines of evidence suggest that the light generated by organisms when they come in direct contact with the nets or encounter turbulence caused by the net is used by individuals ahead of the net to detect its presence and begin an avoidance response. It seems likely that the light ahead of the net observed by Boden (1969) was caused by the same kind of response mechanism described by Neshyba (1967), i.e., flashing in response to flashing.

The tactic of reducing the visual contrast between a net and the surrounding water was demonstrated by LeBrasseur and McAllister (unpublished data cited by Clutter and Anraku 1968) to reduce the avoidance error for euphausiids both day and night. However, if bioluminescence in and ahead of the net is an important cue as we suspect it to be, then a more active means of camouflaging the net is required.

It is known from recent evidence (Warner et al. 1979) that decapod crustacea living at the same depth as *N. megalops* are easily "blinded" by even moderate amounts of light. This suggests the possibility of equipping the mouth of a net with a "blinding" light system to be used to periodically illuminate a region ahead of the net with enough light to temporarily blind individuals in the net. With the light out, individuals so affected by the light pulse would be unable to see and, therefore, to respond to the much lower light generated by zooplankton being captured by the net. We postulate that individuals outside the zone of temporary blindness may respond by electing a startle response, but, because the volume illuminated would be so large, their movement would be random with respect to the volume to be filtered by the net. Clearly, considerably more research is required before this strategy could be considered feasible.

There are two precautionary notes that must be made. First, in spite of avoidance error, vertical distribution patterns obtained in sampling this species with MOCNESS at different times under different hydrographic regimes are replicable (Fig. 3). That is, although avoidance error is strongly affecting the numerical estimates, the shape of the vertical distributions seem much less affected. Thus, in spite of the avoidance, we believe we are obtaining valuable ecological in-

formation about this species. Second, for most species of euphausiids and many copepods, chaetognaths, and pteropods in our collections, we have no evidence that differential day/night avoidance is taking place. Therefore, for many ecological studies of oceanic zooplankton, nets still seem the most effective tool to use to quantitatively collect them.

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AGE AND GROWTH OF A PLEURONECTID, *PAROPHRYS VETULUS*, DURING THE PELAGIC LARVAL PERIOD IN OREGON COASTAL WATERS

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ABSTRACT

The age of 331 field-collected English sole, *Parophrys vetulus*, larvae, 3.1-20.0 mm SL, was determined using daily otolith growth increments. Age in days from hatching was estimated by adding 5, the number of days prior to first increment formation in the laboratory, to the number of increments counted on sagittae. Number of otolith growth increments among larvae of known age in the laboratory ranged widely. Yet daily periodicity of increment formation in *P. vetulus* was inferred from the observations that even under poor growing conditions some larvae added one increment each day since first formation and that, unlike the remaining laboratory-reared larvae in which no pattern was evident, increment addition among larvae in the sea appeared to follow a stable and uniform pattern.

Gompertz and von Bertalanffy growth models fitted the resultant size-at-age data equally well; therefore, only the Gompertz model is presented. Larval growth rate decreased from 0.3 mm per day at 8-9 days of age to <0.1 mm per day between 73 and 74 days. The oldest specimen was 74 days old, but most of the larval and transforming specimens collected in plankton samples were <70 days old.

Previous estimates of age at length of larval *P. vetulus*, based on length-frequency modal progression analysis, overestimated the age of larvae >5.5 mm SL by 2-3 times and, correspondingly, the duration of pelagic life was overestimated, 18-20 weeks compared to 8-10 weeks based on otolith-estimated age.

Saccular otoliths grow by addition of layers of material differing in the relative amount of the protein, otolin, and calcium carbonate in the aragonite form (Degens et al. 1969; Pannella 1971). This results in growth units or increments composed of an inner light band and an outer dark band. Once the cycle of formation has been established for a species, otolith growth increments can be used to estimate a fish's age and as a record of its past growth. Daily periodicity of increment formation has been confirmed in numerous species by the number of first-order growth increments within annuli in fish over 1 yr of age (Pannella 1971, 1974), by inspection of otoliths from reared fish of known age (Brothers et al. 1976; Taubert and Coble 1977), or from fish maintained in the laboratory for a known period of time (Struhsaker and Uchiyama 1976). Bands of daily increments are often grouped into fortnightly and monthly growth patterns (Pannella 1974; Rosenberg 1980). Subdaily increments, which appear faint and indistinct, when compared to daily increments, have been found in some species (Taubert and Coble 1977; Brothers and McFarland in press).

The daily increment method of aging larval and juvenile fishes can be used in fishery research to document the timing and duration of spawning, development, and major life history stages and events. The singlemost important application is the accurate determination of growth rates during early life in the sea. This technique has been applied to relatively few species, however, and much remains to be learned about how growth may change during development and under varying environmental conditions. Once specific growth rates are available, age-dependent larval mortality rates can be estimated and used to improve estimates of spawning stock biomass and also, perhaps, provide insight into recruitment success.

This paper documents the existence of daily growth increments in laboratory-reared and field-caught larvae of an eastern North Pacific pleuronectid, the English sole, *Parophrys vetulus*. It provides the first accurate estimates of

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age at length for larvae of this species and describes the growth of larvae collected in Oregon coastal waters during the 1977-78 spawning season. It is the first detailed study of larval growth of a pleuronectid throughout the pelagic period, and further, provides a basis for the documentation of growth during transformation to the adult form (Rosenberg and Laroche 1982) and of juveniles in nursery grounds off the Oregon coast (Rosenberg 1980).

METHODS

Spawning and Rearing Procedures

Ripe adult *P. vetulus* were collected during fall and winter 1978 with a 12 m otter trawl off the Oregon coast in the vicinity of Hecata Head, approximately lat. 44°10'N, long. 124°18'W, 68-77 m water depth. Eggs were artificially fertilized on shipboard (Bagenal and Braum 1971) and transported back to the laboratory in seawater-filled plastic bags.

In the laboratory, eggs were incubated and larvae reared at 12°-13°C and under a 14-h light, 10-h dark photoperiod in filtered seawater taken from the area where the adults were captured. Eggs held in 4 l glass jars hatched in 3-3½ d. The newly hatched larvae were transferred by pipette to new 4 l glass jars or 8 and 9 l plastic tubs in which a bloom of the green flagellate *Tetraselmis* sp. was maintained throughout the rearing period. Approximately every 2 d, one-fourth to one-third of the water in rearing containers was replaced. On day 4 after hatching, *Gymnodinium splendens*, a naked dinoflagellate, and *Brachionus plicatilis*, a rotifer, were introduced into the rearing containers. After 1-2 wk, *G. splendens* was no longer added because larvae did not appear to eat this organism. Prey concentrations were not measured but *B. plicatilis*, the primary food item, was maintained at high levels, i.e., rotifers were readily visible throughout rearing containers. *Artemia salina* nauplii and the harpacticoid copepod, *Tisbe* sp., provided secondary food sources.

One to ten larvae were preserved in ~80% ethanol each day after hatching for the first 35 d; subsequently, older larvae were preserved at irregular intervals. Larvae were reared from two separate spawnings, in early and late fall 1978, but since rearing conditions were identical, age and growth data from the two were combined.

Field and Laboratory Procedures

Parophrys vetulus larvae were collected in the field with 70 cm, 0.505 mm mesh bongo nets in bottom to surface stepped, oblique tows. Samples were taken approximately monthly from November 1977 to June 1978 in Yaquina Bay, Oreg., and 2-7 km offshore (lat. ~44°37'N; long. 124°05'W). Samples were drained and preserved in ~80% ethanol; within 12-18 h the samples were drained again and fresh preservative was added. With each plankton sample surface temperature, surface and bottom salinity were recorded and a bathythermograph cast was made.

In the laboratory all fish larvae were removed from plankton samples and stored in ~80% ethanol. Otoliths were removed from *P. vetulus* larvae within 6 mo of initial preservation because longer storage resulted in erosion or complete dissolution of the otoliths.

Prior to otolith removal *P. vetulus* larvae were placed in freshwater for ~1-2 min (somewhat longer for specimens >15 mm) to remove or dilute ethanol in the tissue. A larva was then placed in a drop of water on either a glass slide or large rectangular cover slip under a dissecting microscope fitted with polarizing filter and analyzer. Standard length (SL) was measured with an ocular micrometer to the nearest 0.1 mm and both sagittae were dissected out with fine probes at 25 × or 50 × magnification. The larva was removed from the slide or slip and the otoliths were left to dry concave side up. Sagittae were then permanently mounted under a cover slip with Pro-Texx,[3] a clear mounting medium. Rectangular cover slip mounts, which were thought to improve the optical properties of the preparation, were taped for support to a thin piece of brass for viewing under the microscope.

Otolith growth increments, consisting of an inner light band and a narrower, sharply delineated, continuous outer dark band adjacent to it, were counted using a compound microscope with bright field illumination at 800 × or 1,250 × magnification. Faint bands inside the otolith nucleus in reared larvae and "subdaily" or weak rings between well-defined growth increments in some older (>30 d old) field-caught fish were not counted. Counts were made on only one sagitta of the pair and were repeated until a

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

final, "best" count was reached. Successive counts and verification counts which were made by the original reader at a later time usually did not vary by more than ±2. Age estimates could not be obtained for 10% of the field-caught larvae because increments were faint and indistinct or the otoliths were misshapen. Maximum otolith and nucleus diameters were measured to the nearest micron. Photomicrographs were taken at 500 × or 1,000 × magnification under a light microscope.

Shrinkage of larvae preserved in 80% ethanol was compared with shrinkage after preservation in 10% seawater-diluted Formalin, the fixative most commonly used to preserve plankton samples. Thirty 7-day-old reared larvae were measured alive and immediately preserved in either 80% ethanol (15) or 10% Formalin (15). The live, mean standard lengths of the two groups of larvae were 4.34 and 4.42 mm. After 4 mo in preservative the mean standard length of the ethanol-preserved group was 4.20 mm and of the Formalin-preserved group, 4.196 mm. Mean percent shrinkage or 100(original SL − preserved SL/original SL) was 3.2% in the ethanol-preserved group and 5.1% in the Formalin-preserved group. The difference in amount of shrinkage between the two groups was highly significant (ANOVA, $P<0.01$). Care must be taken, therefore, when comparing estimates of size at age based on measurements of larvae preserved in different fixatives. From this limited investigation it became apparent that Formalin-preserved *P. vetulus* larvae appear to be somewhat smaller at age than ethanol-preserved fish.

Statistical Procedures

Gompertz and von Bertalanffy growth models were fitted to larval *P. vetulus* data because the form of the length-age plot was nonlinear with a distinct upper asymptote. A detailed discussion of the Gompertz function, which is the primary model used in this paper, and methods for obtaining initial parameter estimates are presented by Zweifel and Lasker (1976). The generalized equation of this model is:

$$L_t = L_0 \exp\left[K\left(1 - e^{-\alpha t}\right)\right],$$

where L_t = length at age t; L_0 = length at $t = 0$ (i.e., where the curve intercepts the y-axis); and $K = \frac{A_0}{\alpha}$, or the specific growth rate at $t = 0$ divided by the rate of exponential decay. Untransformed data were used in this model because the standard deviation of larval lengths at age remained relatively constant and did not increase with age, indicating variance homogeneity within the data set. The Gallucci and Quinn (1979) version of the von Bertalanffy equation was employed, utilizing the new parameter, $w = kL_\infty$, where k is the growth constant, and L_∞, the asymptotic maximum size, which for *P. vetulus* larvae is the maximum size attained in the plankton prior to transformation into benthic juveniles. The general form of this equation is:

$$L_t = \frac{w}{k}\left\{1 - \exp\left[-k(t - t_0)\right]\right\},$$

where t_0 is the time when $L_0 = 0$ (i.e., where the curve intercepts the x-axis).

The SPSS NONLINEAR[4] program employing Marquardt's algorithm was used to fit both models. A measure of goodness of fit was provided by the residual sums of squares (RSS), the standard error of the regression (or standard deviation of the residuals), and approximate 95% confidence limits for each parameter assuming linearity. Linear confidence theory can be applied here because the assumption of linearity at the final (least squares) parameter values is a reasonable one (Conway et al. 1970; Kimura 1980). A comparison of the RSS at the final parameter values to the linear estimate RSS provides a measure of the linearity of the sum of squares (SS) function (SPSS NONLINEAR program).

Absolute growth rate or $\frac{L_2 - L_1}{t_2 - t_1}$ expressed in millimeters per day and specific growth rate or $\frac{\ln L_2 - \ln L_1}{t_2 - t_1} \times 100$ expressed as percent per day of length were calculated (Ricker 1979).

RESULTS

Increment Formation

Parophrys vetulus larvae survived and grew in the laboratory for over 35 d after hatching, with some individuals eventually transforming into juveniles. However, growth after yolk-sac absorption, between days 4 and 5, was retarded and

[4]SPSS NONLINEAR. Statistical Package for the Social Sciences, Vogelback Computing Center, Northwestern University, Evanston, IL 60201.

not comparable to growth in the field. Despite this, growth increments were visible on the otoliths of over 300 reared larvae. Increments, though extremely narrow and crowded, were even visible on the otoliths of larvae as old as 54 d.

In the laboratory, the highest incidence of larvae with one growth increment occurred on days 5 and 6 (Table 1; Fig. 1a, b). This coincided with the time that larvae first began to swim actively near the surface of rearing containers and search for food. By day 5 larvae had also acquired darkly pigmented, iridescent eyes and functional mouths, and had utilized all or almost all their yolk. Age at first increment formation in the field was ascertained by comparing mean otolith diameter (μm) of field-caught larvae with a single increment, to mean otolith diameter of laboratory-reared larvae of known age (Table 1). The otolith diameter, 23.8 μm, of field-caught larvae with only one growth increment ($\overline{SL}$ = 3.7 mm) fell between the mean values for laboratory-reared larvae at 5 d, 23.1 ($\overline{SL}$ = 4.2 mm), and at 6 d, 24.2 ($\overline{SL}$ = 3.9 mm). Age of all field-caught larvae with one otolith growth increment was, therefore, taken to be 6 d. Age at first increment formation varied among individuals in the laboratory and may, likewise, vary in the field; however, for the purpose of developing a generalized growth model, a single, best estimate of this event was made. The apparent smaller size of field-caught larvae with one increment most likely resulted from shrinkage during capture prior to preservation (Theilacker 1980). Larvae sampled in the laboratory were pipetted alive directly into preservative, thus reducing the amount of handling-induced shrinkage.

Although laboratory results were somewhat ambiguous, daily periodicity of otolith growth increment formation in *P. retulus* was inferred from the following observations: 1) despite less than optimum rearing conditions some 14-, 17-, and 20-d-old larvae had added one increment each day since first formation on day 4 (Table 2); 2) no other periodical pattern in increment formation (i.e., other than daily) was observed among laboratory-reared larvae; 3) increment addition among larvae in the sea appeared to follow a stable and uniform pattern. The wide range in number of otolith increments among reared larvae of known age may have been caused by poor growing conditions which resulted in stunted body and otolith growth (Table 2). Reared larvae of northern anchovy also failed

FIGURE 1.—Photomicrographs of *Parophrys retulus* otoliths (× 1,000). a. Sagitta (22 μm in diameter) prior to first increment formation from a 4-d-old, laboratory-reared larva; b. Sagitta (24 μm in diameter) with two complete increments (highlighted with black lines) from a 6-d-old, laboratory-reared larva; c. Sagitta (22 μm in diameter) with two complete increments (highlighted with black lines) from a 7-d-old, field-caught larva.

TABLE 1.—Comparison of mean otolith diameters (OD) of laboratory-reared and field-collected *Parophrys vetulus* larvae. Age of reared larvae represents days from hatching.

Age (days)	Mean OD (μm)	No. larvae	No. growth increments 0	1	2	3	4	Mean OD (μm)	No larvae	No. growth increments
0	14 6	10	10							
1	16.6	12	12							
2	18.8	10	9	1						
3	20 5	11	10		1					
4	21 6	14	13		1			21.3	7	0
5	23 1	24	10	10	4			23.8	4	1
6	24 2	19	4	4	8	2	1	24 6	10	2

to consistently form growth increments when maintained on low rations (Methot and Kramer 1979). In *P. vetulus*, delayed inception of increment formation, up to 8 d after hatching, may also have accounted for some of the apparent irregularity in increment formation in the laboratory (Table 2). Another factor contributing to ambiguity of laboratory results was the difficulty in counting otolith increments in older larvae. Increments in most laboratory-reared fish after 16-25 d were exceedingly faint and, in some fish, no increments could be discerned (Fig. 2a, b). Growth increments were, in general, clearer and more distinct on the otoliths of field-caught *P. vetulus* larvae than on otoliths of laboratory-reared fish (Figs. 1c, 2c). The steady increase in number of increments with increasing otolith diameter and length of pretransformation larvae in the field is evidence that the irregularity in increment formation observed in the laboratory did not occur under natural feeding conditions (Figs. 3, 4).

Age and Growth

Age of field-caught *P. vetulus* larvae in days from hatching was estimated by adding 5, the number of days prior to appearance of the first otolith growth increment, to the number of increments counted on sagittae. Counts of growth increments were obtained from 338 larval and transforming, pelagic specimens ranging from 2.4 to 20.0 mm SL (Fig. 4). But age could be estimated for only 331 larvae because increment formation had not yet begun in seven small specimens, 2.4-3.7 mm SL (Fig. 5). The oldest *P. vetulus* taken in plankton samples during 1977-78 was 74 d (2.4 mo) old and 17.8 mm SL. The next oldest larvae ranged from 65 to 70 d old and were 19-20 mm SL. The length of pelagic life of *P. vetulus* can be estimated directly from these data to be 2-2.5 mo. Few *P. vetulus* larvae >20 mm SL, the size at which larvae transform to benthic juveniles (Ahlstrom and Moser 1975; Rosenberg and Laroche footnote 3), were taken in extensive plankton collections off Oregon during the spring months in 1972-75 (Laroche and Richardson 1979). The largest larva taken in those collections was 22 mm SL.

Behavior of reared *P. vetulus* larvae further supports a pelagic phase of 2+ mo. At approximately 60 d of age, larval *P. vetulus* maintained in the laboratory first exhibited the tendency to rest on their sides on the bottom and to swim with their bodies at an angle to the vertical (J. L. Laroche unpubl. data).

TABLE 2.—Summary of growth in body length (SL) and otolith diameter (OD), and counts of growth increments on otoliths of laboratory-reared *Parophrys vetulus* larvae. *N* = number of larvae from which growth increment counts were taken; (*N*) = number of larvae used in mean otolith diameter calculation.

Age (days)	*N*	Mean SL (mm)	Range SL (mm)	Mean OD (μm)	Range OD (μm)	No. growth increments Mean	Range
4	14	4.1	3.7-4.4	21.6	20-25	0	0-2
5	24	4.2	3.8-4.5	23.1	20-25	1	0-2
6	19(17)	3.9	3.1-4.2	24.2	23-27	2	0-4
9	9	4.0	3.7-4.1	24 7	23-26	3	2-4
10	13	4 2	3.7-4.6	25.7	25-27	4	3-6
14	13	4.9	5.8-4 2	28.7	27-33	8	5-10
17	13	5.4	4 5-6.3	29.6	28-33	10	5-13
20	7(6)	5.7	5.1-6.4	31.8	30-36	10	5-16
21	6	5.9	5.4-6.6	31.2	30-34	13	10-16
26	18(17)	7.0	5.6-8.6	33.4	30-37	14	10-20

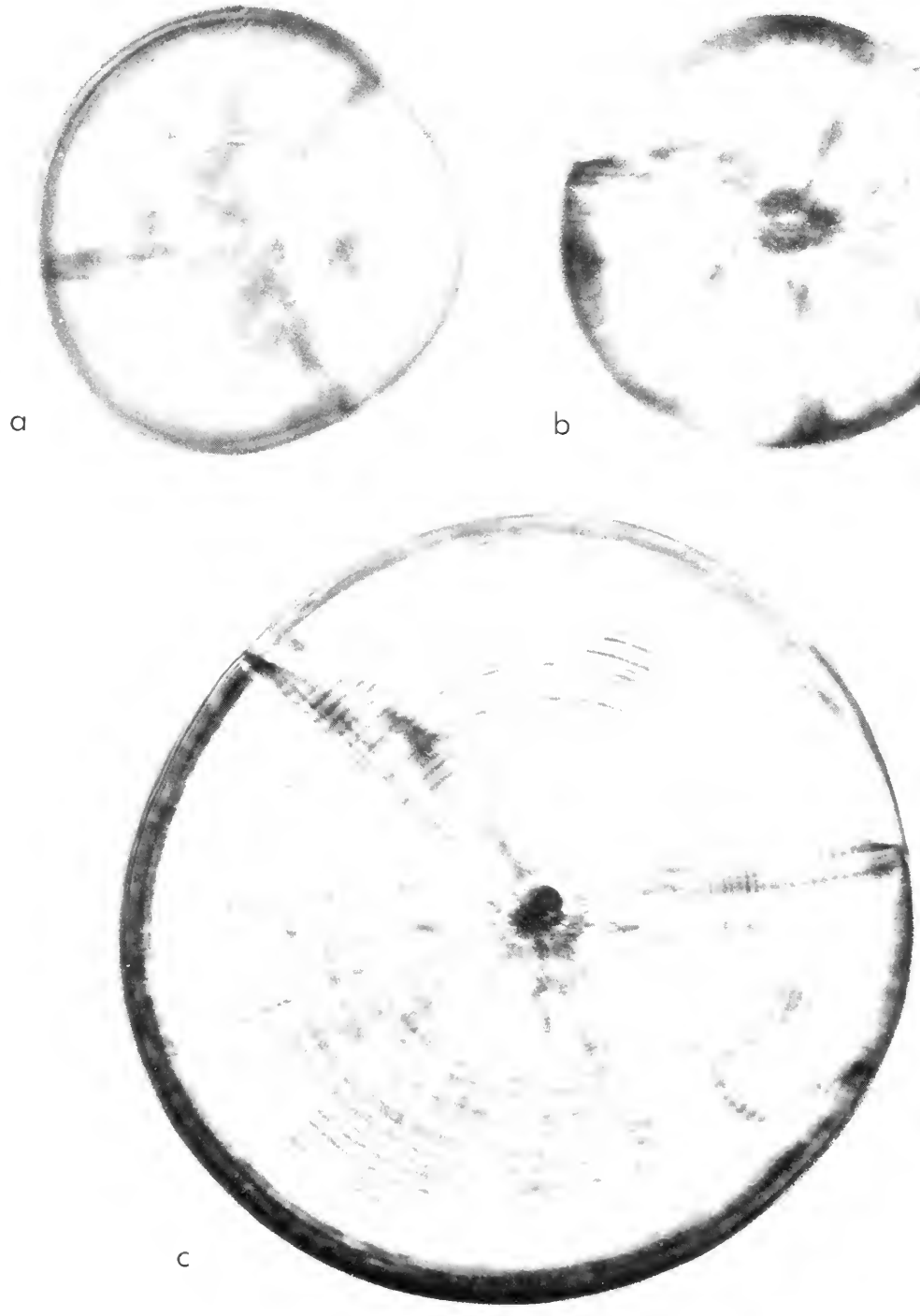

FIGURE 2.—Photomicrographs of *Parophrys vetulus* otoliths (×1,000). a. Sagitta (30 μm in diameter) with 16 complete increments from a 21-d-old, laboratory-reared larva; b. Sagitta (32 μm in diameter) with no discernible increments from a 22-d-old, laboratory-reared larva; c. Sagitta (102 μm in diameter) with 42 complete increments from a 47-d-old, field-caught larva.

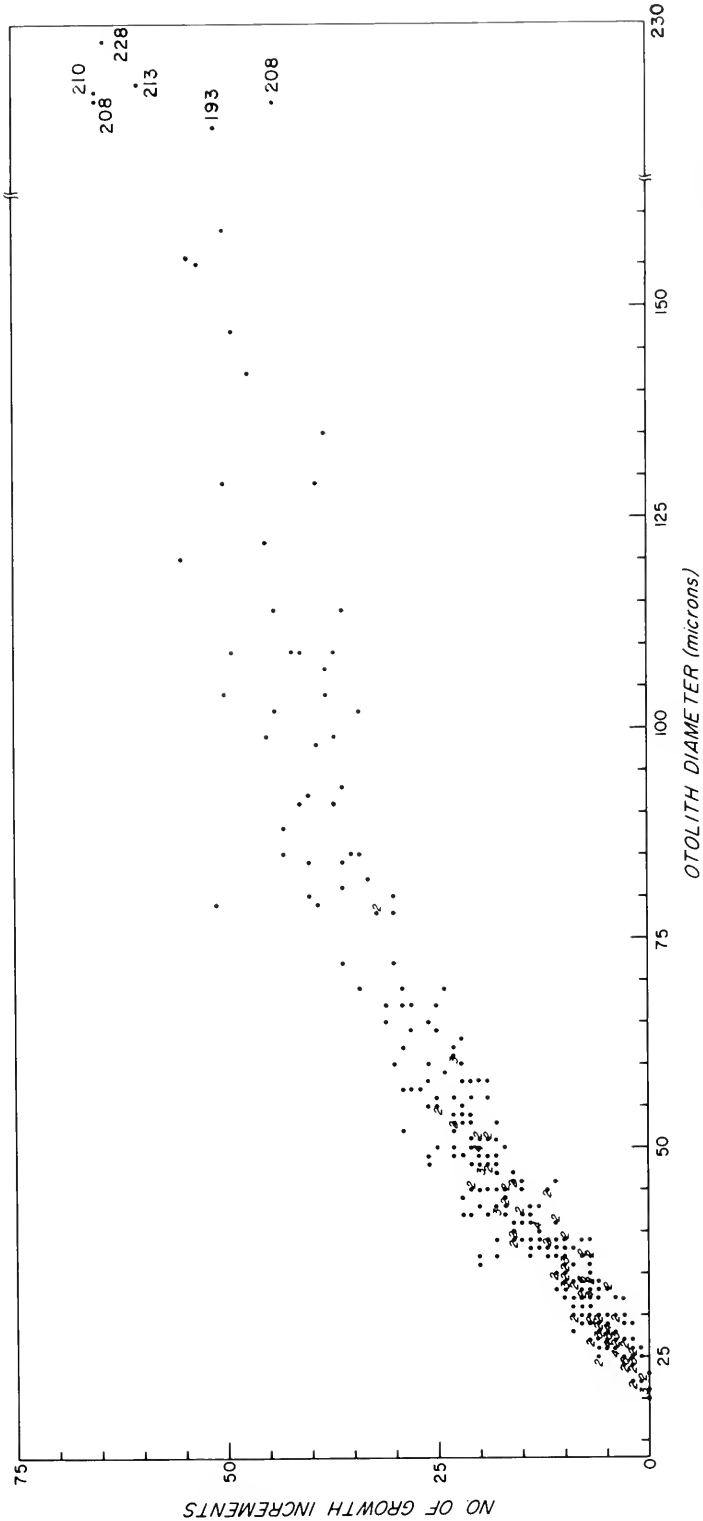

FIGURE 3.—Number of otolith growth increments related to otolith diameter of 338 larval and transforming, field-caught *Parophrys vetulus*.

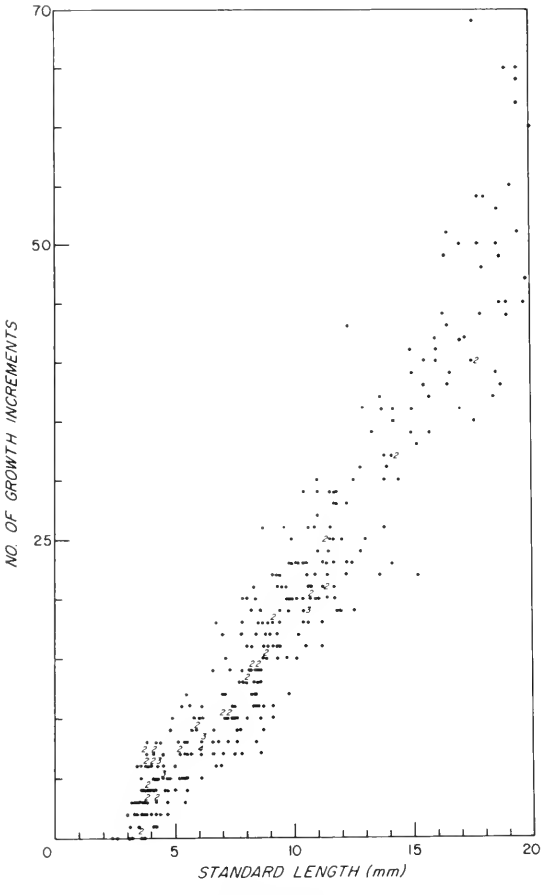

FIGURE 4.—Number of otolith growth increments related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

Our description of early growth of *P. vetulus* in Oregon coastal waters at temperatures ranging from 9° to 11°C is based on the ages and lengths of 331 specimens, 3.1-20.0 mm SL, with otolith growth increments. Gompertz and von Bertalanffy models yielded good and nearly identical fits to the data and similar estimates of growth rate; therefore, the results of only one model (Gompertz) are presented (Table 3; Fig. 5). RSS and linear estimate RSS of the Gompertz growth parameters were very similar; thus, the assumption of linearity in computing 95% confidence limits is reasonable, and the computed limits indicate relatively narrow confidence regions around the parameters (Table 3).

Previous estimates of age at length of larval *P. vetulus* were derived from the progression of modes in length-frequency distributions of larvae from a time series of (10% Formalin preserved) plankton samples (Laroche and Richardson 1979). A comparison of those results with age at length estimated by the Gompertz equation (Zwiefel and Lasker 1976) indicates that the length-frequency method overestimated the age of larvae >5.5 mm SL by 2-3 times (Table 4).

Estimates of specific and absolute rates of growth were calculated from length at age for various ages as predicted by the Gompertz model (Table 5). Specific growth rate steadily decreased between 8 and 74 d. Absolute growth rate was fairly uniform between 8 and 31 d, slowed somewhat between 31 and 41 d, but was more drastically reduced between 73 and 74 d, at which time larvae undergo transformation, a

TABLE 3.—Gompertz equation and estimated parameters describing the growth of 331 *Parophrys vetulus* larvae in Oregon waters during the 1977-78 spawning season. RSS = residual sum of squares; SE = standard error of the regression; S^2 = variance; CL = confidence limits.

Equation: $L_t = 2.073 \exp\left[2.354\,(1-e^{-0.045t})\right]$; Linear est. RSS = 564.892; RSS = 520.83; SE = 1.256

Parameters	S^2	RSS	Approximate 95% CL
$L_0 = 2.073$	0.023	564.892	$L_1 = 1.779$, $L_2 = 2.367$
$K = 2.354$	0.003	535.762	$L_1 = 2.245$, $L_2 = 2.462$
$\alpha = 0.045$	0.00001	533.854	$L_1 = 0.040$, $L_2 = 0.050$

TABLE 4.—Age of *Parophrys vetulus* larvae; (*A*) estimated from modal progression in length-frequency distributions of larvae caught during 1971 in biweekly and weekly Formalin-preserved plankton samples (Laroche and Richardson 1979), (*B*) estimated by the Gompertz equation based on otolith increment counts from ethanol-preserved larvae caught in 1977-78.

SL (mm)	Estimated age (weeks) (*A*)	(*B*)
5.5	2.3	1.7
7.5	4.1	2.5
9.5	5.9	3.3
11.5	8.7	4.1
13.5	13.4	5.0
15.5	17.6	6.1
17.5	21.9	7.5

TABLE 5.—Growth rates of *Parophrys vetulus* larvae predicted from the Gompertz equation at various times from hatching.

Age (days)	Specific growth rate (% per day SL)	Absolute growth rate (mm per day)
8-9	7.3	0.32
15-16	5.3	0.36
19-20	4.4	0.36
24-25	3.5	0.35
30-31	2.7	0.33
40-41	1.7	0.25
73-74	0.4	0.08

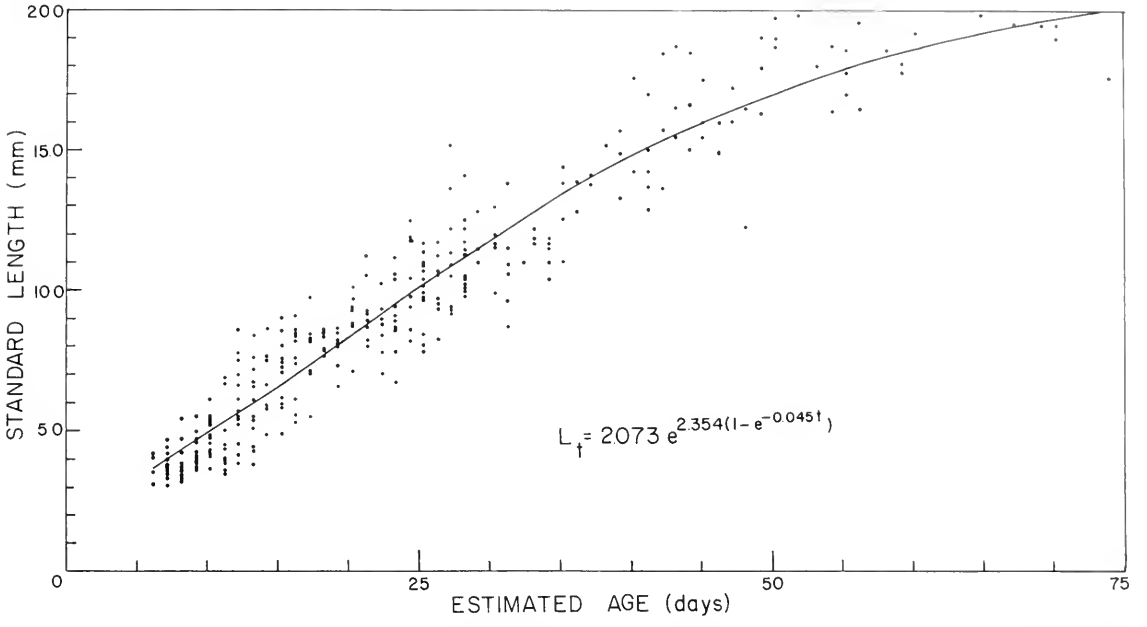

FIGURE 5.— Gompertz curve and equation fitted to length at age of 331 larval and transforming, field-caught *Parophrys vetulus* with at least one otolith growth increment.

period characterized by reduced growth in length (Rosenberg and Laroche 1982).

The plot of otolith diameter on standard length of pelagic larval and transforming *P. vetulus* revealed an allometric relationship (Fig. 6). A distinctive feature of this plot was the apparent continued, even accelerated growth of sagittae as *P. vetulus* larvae reached the size of transformation, 18-20 mm SL, when rate of growth in body length slows down. Physical evidence of accelerated growth in otolith diameter relative to body length can be seen by the increased width of the outermost increments on otoliths of larvae older than 30 d (e.g., outer 9-10 increments on sagitta in Fig. 2c). The otolith diameter to standard length relationship, once a mathematical formulation has been computed, can be used to back-calculate individual growth histories of larvae and juveniles (Rosenberg 1980; Methot in press), as has been done for adult fishes (Tesch 1968; Ricker 1969).

DISCUSSION

As in numerous other temperate and some tropical species of fishes, growth increments on the otoliths of *P. vetulus* larvae appear to be formed daily after yolk-sac absorption when larvae become capable of exogenous feeding. Counts of these increments provide more precise and accurate estimates of larval age and growth rates throughout the larval period than have previously been available. This information, when combined with abundance data, allows computation of age-dependent mortality rates resulting in more accurate estimates of larval mortality in the sea.

Empirically, both the Gompertz and von Bertalanffy growth models fit the larval *P. vetulus* data well. Both yielded similar values for length at age and growth rates from which age-dependent mortality estimates can be made. There has been much disagreement, on theoretical grounds, as to the appropriateness of either model for describing growth in fishes, although they are mathematically quite similar (e.g., Zweifel and Lasker 1976; Ricker 1979). Despite numerous attempts to attribute biological significance to mathematical models of growth, the best criterion available for choosing a particular model is still goodness of fit to the data (Ricker 1979). In that respect, both models were appropriate to this data set.

A practical measure of the appropriateness of mathematical models is the relative accuracy and stability of pertinent parameter estimates (Gallucci and Quinn 1979). In the Gompertz

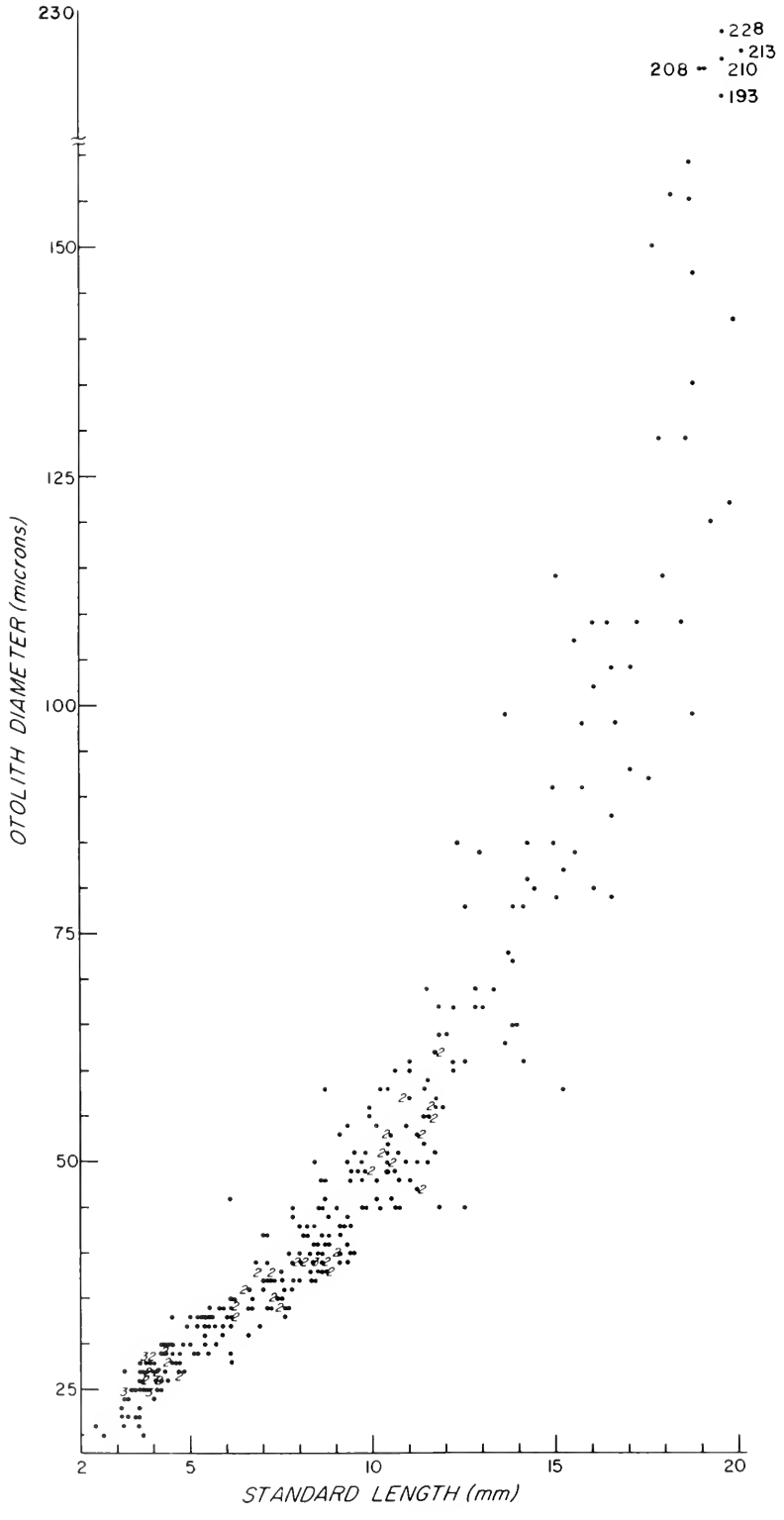

FIGURE 6.—Otolith diameter related to standard length of 338 larval and transforming, field-caught *Parophrys vetulus*.

model, the parameter L_0 or the y-intercept has been used as an estimator of length at hatching (Zweifel and Lasker 1976). However, the value of this parameter, 2.07 mm SL, for the *P. vetulus* data set was low compared to mean hatching lengths of reared larvae: 2.60 ($N = 11$) and 2.91 ($N = 10$) mm SL at 12°-13°C (Laroche unpubl. data); and 2.85 ($N = 25$) mm TL at 10°-11°C (Orsi 1968). Net-caught larvae on which the growth model is based would appear smaller at age because of increased shrinkage during capture (Theilacker 1980). This may account for some of the difference in predicted and observed hatching lengths. Another probable cause of this discrepancy is the lack of data points in the <6 d of age region of the plot, i.e., before growth increment formation begins. The value of L_0 is based on extrapolation beyond the actual data and may be, therefore, of questionable use as a measure of the appropriateness of this model.

Comparison with larval growth in the field at similar temperatures of another pleuronectid, *Pseudopleuronectes americanus*, provided evidence that growth rates predicted by the Gompertz model for *Parophrys vetulus* are realistic. Larval *Pseudopleuronectes americanus* between the ages of 28 and 42 d, growing in large enclosures in Narragansett Bay at 10°-15°C, had a specific growth rate of 1.9% per day of standard length (Laurence et al. 1979). The predicted specific growth rate of *Parophrys vetulus* of the same age, growing at 9°-11°C, was 2.2%. Larval *Pseudopleuronectes americanus* between 28 and 42 d of age grew from 6.6 to 8.6 mm SL, while *Parophrys vetulus* larvae grew from 11.2 to 15.3 mm SL. Although these two species differ in size at age, both transform at approximately the same age, 8-10 wk, and appear to grow at similar rates between 4 and 6 wk of age. Since length at hatching, ~2-3 mm SL, is similar for both species, higher rates of growth prior to and after 4-6 wk probably accounts for the greater size at age of *P. vetulus* and greater size at transformation, >18 mm SL in *P. vetulus* versus <10 mm for *Pseudopleuronectes americanus*.

A comparison of otolith-estimated and length-frequency derived age-at-length data indicated that the latter method overestimated age of *Parophrys vetulus* larvae >5.5 mm SL by 2-3 times. This resulted in a gross overestimate of duration of the pelagic life of this species, 18-22 wk (Laroche and Richardson 1979) compared to 8-10 wk based on the age data presented here. It is unlikely that these large differences are solely the result of different preservatives. Such a large discrepancy between the two methods demonstrates the serious inaccuracies that could result from attempts to estimate age and growth rates from length-frequency data. Such data predictably yield low estimates of growth, especially for species with protracted spawning, because of continual recruitment of small larvae to the population. Problems of net avoidance by larger specimens further bias length-frequency distributions.

The otolith aging method developed in this study could be used further to investigate growth and survival among different cohorts of *P. vetulus* larvae. Spawning in this species is highly variable in both frequency and timing (Laroche and Richardson 1979). Peak spawning can be bimodal in some years with a 2-4 mo separation between peaks (Kruse and Tyler[5]). Larvae produced in those two peaks could develop and grow under very different temperature regimes and feeding conditions, which could result in two distinct groups of larvae differing in rates of growth, mortality, and relative contribution to that year class.

ACKNOWLEDGMENTS

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Rindy Ostermann and Betsy B. Washington assisted in all phases of collection of ripe adult specimens, larval rearing, otolith removal, and data compilation. Rae Deane Leatham and Percy L. Donaghay instructed the first author in culture techniques and generously provided the equipment and space in their laboratory for parts of this work. Eric Lynn, National Marine Fisheries Service, NOAA, La Jolla, Calif., sent us cultures of larval food organisms. Gary Hettman, Oregon Department of Fish and Wildlife, kept us informed throughout the fall and winter of the likely locations of English sole spawning concentrations. Waldo W. Wakefield and Marky Bud Willis assisted at sea in collecting spawning fish. Chip Hogue, Paul Montagua, Gene Ruff, and Andrew Carey provided laboratory space

[5]Kruse, G. H., and A. V. Tyler. 1980. Influence of physical facotrs on the English sole (*Parophrys vetulus*) spawning season. Unpubl. manuscr., 25 p. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR 97331.

and their microscope for otolith observations. Otolith photomicrographs were taken with the help and guidance of Michael D. Richardson, Naval Ocean Research and Development Activities, Bay St. Louis, Miss.

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PHENOTYPIC DIFFERENCES AMONG STOCKS OF HATCHERY AND WILD COHO SALMON, *ONCORHYNCHUS KISUTCH*, IN OREGON, WASHINGTON, AND CALIFORNIA[1]

R. C. Hjort and C. B. Schreck[2]

ABSTRACT

Similarities in phenotypic characters (isozyme gene frequencies, life history, and morphology) among 35 stocks of coho salmon, *Oncorhynchus kisutch*, from Oregon, Washington, and California were compared by using agglomerative and divisive cluster analyses. Coho salmon stocks from similar environments were phenotypically similar. Five groups of stocks were identified by the agglomerative cluster analysis: 1) wild stocks from the northern Oregon coast, 2) wild stocks from the southern Oregon coast, 3) stocks from hatcheries that used wild coho salmon for an egg and sperm source, 4) stocks from large stream systems, and 5) hatchery stocks from the northern Oregon coast. Three trends were indicated by the clustering patterns: 1) stocks that were geographically close tended to be phenotypically similar, 2) stocks from large stream systems were more similar to each other than to stocks from smaller stream systems, independent of geographic proximity, and 3) hatchery stocks were more similar to each other than to wild stocks, and wild stocks were more similar to each other than to hatchery stocks. These trends may be useful to fishery managers for selecting donor stocks from hatcheries for transplanting to stream systems or transferring to other hatcheries. Individual phenotypic characters were correlated with characters of the stream systems. Results of two agglomerative cluster analyses, one of certain characters of the stocks and one of certain characters of the stream systems, demonstrated a lack of correspondence between stream types and stock phenotypes.

Genetic diversity among stocks of anadromous salmonids (Simon and Larkin 1970) is a biological characteristic that is more frequently discussed than used in fishery management. The tendency to return to native streams reduces gene flow among salmon populations and enables the individual stocks to adapt to the native stream systems. The mixing of stocks highly adapted to their native stream systems with other stocks, or transplanting them to other stream systems, may reduce the rate of return or survival rate of the donor stock (Ritter 1975[3]; Bams 1976). If the survival rate of a salmon stock is related to its degree of adaptation to its stream system, fishery managers may be able to increase survival of hatchery fish by planting them in recipient streams having native stocks genetically similar to the planted fish. Higher survival should be especially important during the first several generations, while the transplanted stock is adapting to the recipient environment. An additional advantage of using genetically similar stocks might be a reduction in the introgression of divergent hatchery genotypes into wild stocks (Reisenbichler and McIntyre 1977).

Genetic descriptions of salmon stocks could benefit salmon management by assisting fishery managers in selecting hatchery stocks and in protecting wild stocks. Obviously, determination of genetic similarity among stocks is not now possible for the entire genome; however, similarity can be estimated by comparing genetically related characters. Two biochemical characters that vary among stocks of coho salmon, *Oncorhynchus kisutch*, are transferrin (Utter et al. 1970) and phosphoglucose isomerase (PGI) (May 1975), the electrophoretic expressions both of which were established by breeding studies to be genetically determined. Life history and morphological characters also vary among salmonid stocks. Time of spawning (Roley 1973) and frequency of occurrence of jacks in the population (Feldmann 1974) both have a genetic basis in

[1]Oregon State University Agricultural Experiment Station Technical Paper Number 5477.

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[3]Ritter, J. A. 1975. Lower ocean survival ratio for hatchery reared Atlantic salmon (*Salmo salar*) stocks released in rivers other than their native streams. Int. Counc. Explor. Sea, Anadromous and Catadromous Fish Comm., C. M. 1975/M 26, 10 p.

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FISHERY BULLETIN: VOL. 80, NO. 1, 1982.

coho salmon but probably have an environmental component as well. A genetic basis, as shown in rainbow trout, *Salmo gairdneri*, has also been established for numbers of vertebrae (Winter et al. 1980a), scales in the lateral series (Winter et al. 1980a), scale rows (Neave 1944), gill rakers (Smith 1969), branchiostegals (MacGregor and MacCrimmon 1977), and anal fin rays (MacGregor and MacCrimmon 1977). Ricker (1970) hypothesized that the meristic characters of salmonids probably have both genetic and environmental components. The difficulty of determining the importance of these phenotypic characters to the fitness of the stock does not preclude the possibility that they could, through selection or pleiotrophic effects, have a bearing on fitness as suggested by Barlow (1961).

The objective of this study was to characterize stocks of coho salmon by using enzyme gene frequencies, life history characters, and morphological characters. Secondarily, we hoped this information would help provide a basis for selecting donor stocks in Oregon hatchery programs. The stocks were selected so that comparisons could be made among geographical areas and stream types and between hatchery and wild stocks. We calculated a measure of a phenotypic similarity and used cluster analysis to display the relationships among stocks. Because cluster analyses are arbitrary (Blackith and Reyment 1971), we used two clustering strategies. Factors affecting genetic similarity were hypothesized by determining environmental characteristics common to the similar stocks.

Although our analysis is primarily systematic, we correlated the phenotypic characters with variables characteristic of the stream systems. Although correlations do not prove a functional significance, they are included here because inferences and hypotheses can be developed from the correlations for future studies.

METHODS

Sampling

We evaluated 10 characters for 15 hatchery stocks (based on samples of 75-100 juvenile coho salmon of the 1976 brood from 14 hatcheries in Washington, Oregon, and California and 9 hatcheries from Oregon for the 1977 brood year) and 12 wild stocks (based on samples of 30-100 juvenile coho salmon of the 1976 and 1977 broods, collected by electrofishing from 12 Oregon stream systems). (See Figure 1 for locations of hatcheries and stream systems.) Because some of the hatcheries have used nonnative egg sources, and stream systems have been stocked with juvenile and adult coho salmon, few pure native stocks remain. We did not use hatchery stocks or

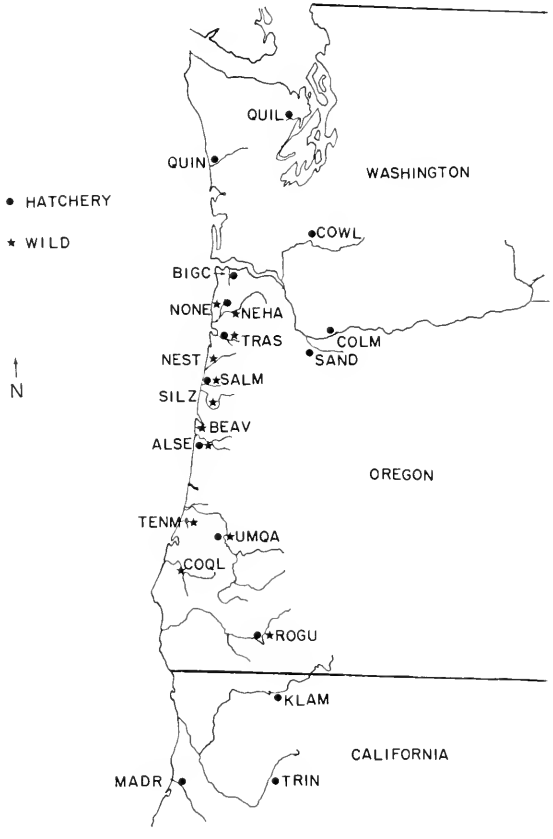

FIGURE 1.—Map indicating sample site locations of wild and hatchery coho salmon stocks. Location codes are as follows with the hatcheries in parentheses: ALSE, Alsea River (Fall Creek Hatchery); BEAV, Beaver Creek; BIGC, Big Creek (Big Creek Hatchery); COLM, Columbia River (Cascade Hatchery in 1976 and Bonneville Hatchery in 1977); COQL, Coquille River; COWL, Cowlitz River (hatchery stock reared at Cascade Hatchery in 1976 and Big Creek Hatchery in 1977); KLAM, Klamath River (Irongate Hatchery); MADR, Mad River (Mad River Hatchery); NEHA, Nehalem River; NEST, Nestucca River; NONE, North Nehalem River (North Nehalem River Hatchery); QUIL, Quilcene River (Quilcene River Hatchery); QUIN, Quinault River Hatchery); ROGU, Rogue River (Cole Rivers Hatchery); SALM, Salmon River Hatchery); SAND, Sandy River (Sandy River Hatchery); SILZ, Siletz River; TENM, Tenmile Lakes; TRAS, Trask River (Trask River Hatchery); TRIN, Trinity River (Trinity River Hatchery); UMPQ, Umpqua River (hatchery stock collected from Smith River and reared at Cole Rivers Hatchery).

fish from tributaries of streams that had received a large supplement of a nonnative hatchery stock in the previous 6 yr. This was to ensure that characterization of the genotype would reflect environmental considerations rather than introgression of foreign stocks.

Morphological Characters

For each sample, 15 carcasses were frozen for later counts. Scales in the lateral series were counted in the second row above the lateral line, starting with the anteriormost scale and terminating at the hypural plate. Scales above the lateral line were counted from the anterior insertion of the dorsal fin to the lateral line. Anal ray counts did not include the short rudimentary anterior rays, and branched rays were counted as one. The total number of gill rakers on the first gill arch was recorded. Alizarin red was used to highlight rudimentary gill rakers. The total number of branchiostegal rays from both sides was counted. Vertebral counts, made on X-ray plates, included the last three upturned centra. Accuracy of morphological counts was checked by recounting two fish from each sample. If errors were found, additional fish from that sample were recounted to correct for any error.

Electrophoresis

Blood and white muscle samples were collected from the fish that were not used for morphological counts. The caudal peduncle was severed and the blood collected in heparinized microhematocrit tubes that were then centrifuged and stored at −10°C. White muscle samples (1 cm^3) were removed from the anterior dorsal portion of the frozen carcasses, homogenized with 2 or 3 drops of water, and then centrifuged to clear the supernatant. Only the blood serum and supernatant were used for electrophoresis.

The methodology for electrophoresis of transferrin and phosphoglucose isomerase followed the basic principles of May (1975) with some modifications by Solazzi.[4] The gel and electrode buffers were described by Ridgway et al. (1970). Four genotypes of transferrin (AA, AC, CC, and BC) in the serum samples were interpreted according to Utter et al. (1970). Transferrin was recorded as the frequency of the "A" allele, since the "B" allele was relatively rare. The variant allele for the second locus of phosphoglucose isomerase, first observed in white muscle tissue by May (1975), was recorded as the frequency of this variant allele.

Life History

The life history characters we used were time of peak spawning and proportion of females in the adult population. We estimated the peak spawning times on the basis of interviews with district fishery biologists and hatchery managers. Whenever possible, we verified the estimates with spawning ground survey records and hatchery records. We stratified the peak spawning times into five segments of 2 wk each.

The proportions of adult females (3 yr olds) were estimated from hatchery records and spawning ground surveys. This character is an indirect measure of the proportion of jacks (males that mature at 2 yr of age) in the population. Populations with high proportions of jacks in a given year should have relatively higher proportions of females returning the next year. A direct measure of the proportion of jacks cannot be used because body size differences between jacks and 3-yr-old adults affect the catch in gill net fisheries, retention in hatchery holding ponds, recovery of carcasses on spawning ground surveys, and catch rate in sport fisheries.

Environmental Data

Stream characteristics include distance upstream to spawning grounds, basin area, area and length of the estuary on the stream system, latitude, gradient, spring runoff, the presence or absence of the myxosporidan parasite, *Ceratamyxa shasta*, and the presence or absence of the following nine species of fish: carp, *Cyprinus carpio*; Oregon chub, *Hybopsis crameri*; northern squawfish, *Ptycholcheilus oregonensis*; speckled dace, *Rhinichthys osculus*; redside shiner, *Richardsonius balteatus*; largescale sucker, *Catostomus macrocheilus*; brown bullhead, *Ictalurus nebulosus*; largemouth bass, *Micropterus salmoides*; and striped bass, *Morone saxatilis*. To separate the populations that have short and potentially long swimming distances to the spawning grounds, we measured spawning distances from the mouth of the stream sys-

[4]Solazzi, M. F. 1977. Methods manual for the electrophoretic analysis of steelhead trout (*Salmo gairdneri*). Oreg. Dep. Fish Wildl., Res. Sect., Inf. Rep. Ser. Fish. 77-7, 35 p.

tem to the upper limit of coho salmon spawning, as estimated from Anadromous Fish Distribution Maps[5] and interviews with district fishery biologists. Inasmuch as, intuitively, latitude should be correlated with the temperature and flow regimes of the stream systems, we determined the latitude at the mouth of each stream system. Gradients were calculated from tidewater to the upper limit of coho spawning as a basis for estimating the difficulty of the spawning migration. Because estuary size and length is an estimate of exposure to vibriosis (Harrel et al. 1976) and potential richness of feeding grounds (Myers 1979), we measured the estuary lengths, stream elevations, and distances on United States Geographical Survey Quadrangle Maps. Inasmuch as high flows could have an effect on both the early life history and the smolting processes of juvenile coho salmon, we determined the presence of a spring runoff from snowmelt by interviewing district biologists. We obtained information on the distributions of other fish species in Oregon stream systems from C. E. Bond,[6] and on the distribution of *Ceratamyxa shasta* from J. E. Sanders.[7]

We obtained temperature data from hatchery records to help interpret the morphological data for the hatchery stocks. The average temperature for the first month of incubation was used, because previous studies have indicated that this time is a period during ontogeny when morphological features may be most sensitive to the effects of temperature (Tåning 1952).

Statistics

We calculated averages for the morphological characters, enzyme gene frequencies, and the proportion of females for each stock, and used multivariate analysis of variance and Rao's (1970) test for additional information to determine whether morphological characters differed significantly among stocks. In Rao's test, the statistical significance of each morphological character is determined, given that the other morphological characters are already in the model. Because environmental data on spawning distance, estuary length, estuary size, basin area, and gradient were skewed, we transformed them to natural logarithms to stabilize the variance and improve normality. We standardized the stock characters ($\bar{z} = 0$, $S^2 = 1$) for the cluster analyses, using the standard normal standardization. This standardization expresses the stock character as standard deviations from the character means, thus giving equal weight to each character.

We calculated correlation coeffients (Snedecor and Cochran 1967) between the stock characters and the environmental data for all stocks, and between the morphological characters and temperature data for hatchery stocks only. The levels of significance for the correlation coefficients were also calculated as described by Snedecor and Cochran (1967).

We used two cluster analysis programs to display similarities among stocks. One, a nonhierarchical divisive cluster analysis, minimized the total sum of squares between observations and the cluster means (McIntire 1973). In the other, a hierarchical agglomerative cluster analysis, Euclidean distance was used as the dissimilarity measure, and the clustering strategy was group average (see Sneath and Sokal [1973] or Clifford and Stephenson [1975] for terminology). Standardized data were used in both programs.

We used canonical variate analysis to investigate the relation among the clusters from the agglomerative cluster analysis (Clifford and Stephenson 1975). Canonical variate analysis produces canonical variables that project groups of multivariate data onto axes separating the groups as much as possible. We plotted the canonical variables against each other in two-dimensional space to determine the relationships among clusters and the discreteness of the clusters.

RESULTS AND DISCUSSION

Morphological Characters

Significant differences ($\alpha = 0.01$) for each morphological character (Tables 1-3) as indicated by multivariate analysis of variance and Rao's test of additional information existed among the 35 samples which consisted of wild and hatchery stocks from two brood years. When morphological characters for each stock between brood years were compared for each of the hatcheries that were sampled in both years of the study

[5]Anadromous Fish Distribution Maps. Oregon State Water Resources Board, Salem, Oreg.

[6]Carl E. Bond, Professor of Fisheries, Oregon State University, Corvallis, OR 97331, pers. commun. April 1979.

[7]James E. Sanders, Assistant Fish Pathologist, Oregon Dep. Fish Wildl., Corvallis, OR 97331, pers. commun. February 1979.

TABLE 1.—Means, standard errors (in parentheses), and ranges for the morphological characters of the 1976 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling locations.

Stock and (in parentheses) incubation water temperatures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchiostegals	Vertebrae
Washington						
Quilcene River Hatchery (7.3)	126.93	28.13	14.07	22.33	27.87	64.40
	(.97)	(.38)	(.15)	(.19)	(.26)	(.13)
	116-132	25-30	13-15	21-23	26-30	64-65
Quinault River Hatchery (7.3)	132.67	29.93	13.53	22.53	26.67	65.50
	(.48)	(.33)	(.16)	(.24)	(.21)	(.13)
	130-136	28-32	13-15	21-24	25-28	65-66
Oregon						
Cascade Hatchery (6.9) (Columbia River)	133.07	28.20	14.00	22.20	27.27	66.80
	(.56)	(.40)	(.20)	(.35)	(.37)	(.22)
	128-135	26-32	12-15	20-25	25-29	66-68
Big Creek Hatchery (6.4) (Columbia River)	132.67	28.80	14.31	22.87	26.07	65.80
	(.57)	(.28)	(.13)	(.17)	(.30)	(.15)
	128-136	28-31	13-15	22-24	24-28	65-67
Cowlitz Hatchery stock, Cascade Hatchery (6.9)	133.60	27.87	13.80	22.20	28.13	64.47
	(.63)	(.24)	(.14)	(.26)	(.24)	(.22)
	131-137	26-29	13-15	21-24	27-30	65-68
Sandy River Hatchery (7.0) (Columbia River)	133.13	28.27	14.33	22.07	28.20	66.07
	(.72)	(.42)	(.13)	(.34)	(.26)	(.21)
	128-137	24-30	14-15	20-25	26-30	65-67
North Nehalem River Hatchery (7.8)	131.93	28.33	14.00	22.67	26.73	65.80
	(.64)	(.30)	(.14)	(.27)	(.32)	(.17)
	128-138	26-36	13-15	21-24	24-28	65-67
Trask River Hatchery (9.8)	132.13	28.80	13.93	22.13	26.40	66.07
	(.48)	(.47)	(.12)	(.31)	(.32)	(.18)
	128-135	26-32	13-15	20-24	24-29	65-67
Salmon River Hatchery (6.2)	129.40	27.00	13.60	22.13	25.40	64.93
	(.54)	(.59)	(.19)	(.24)	(.24)	(.30)
	125-132	23-33	13-15	21-24	24-27	62-66
Fall Creek Hatchery (5.7) (Alsea River)	132.00	28.67	14.00	23.20	27.13	65.80
	(.50)	(.29)	(.17)	(.20)	(.34)	(.17)
	129-135	27-31	13-15	22-25	25-29	65-67
Umpqua Hatchery stock (Smith River), Cole Rivers Hatchery (3.5)	131.20	26.00	13.47	22.13	25.13	65.33
	(.51)	(.34)	(.19)	(.22)	(.24)	(.23)
	127-134	24-28	13-15	21-23	24-26	64-67
California						
Irongate Hatchery (5.3) (Klamath River)	132.73	29.07	13.80	22.33	27.00	66.07
	(.78)	(.18)	(.14)	(.25)	(.28)	(.30)
	129-138	28-30	13-15	21-24	25-28	64-68
Trinity River Hatchery (7.3) (Klamath River)	130.87	28.27	13.60	22.00	26.00	66.00
	(.75)	(.64)	(.13)	(.31)	(.59)	(.14)
	126-137	24-33	13-14	19-23	20-28	65-67
Mad River Hatchery (8.5)	129.20	25.27	13.40	20.93	23.47	65.60
	(.88)	(.37)	(.19)	(.33)	(.51)	(.31)
	121-134	22-27	12-15	19-23	20-27	63-68

(Table 4), the agreement between brood years was not particularly high, especially for scale rows and branchiostegal ray counts.

Although meristic counts and water temperatures during the incubation period of the eggs are usually correlated (Barlow 1961), we found that lateral series scale counts provided the only meristic character significantly ($\alpha = 0.05$) correlated with the temperature of the hatchery water during incubation. Under the extant environmental conditions, incubation temperatures may have little effect in determining the morphological characters of our stocks.

Among all possible statistically significant correlations between morphological characters and the stream characteristics in Table 5, only vertebral number and estuary length, and vertebral number and spawning distance, had correlation coefficients $>r = 0.50$ (Table 6). All other correlations each accounted for <25% of the variation observed. Possibly we overlooked some important environmental gradients, or possibly the selective forces occur during periodic environmental extremes or pulses that were not accounted for in our environmental data. Each of the counts significantly correlated with at least two of the characters of the stream systems, suggesting that, if these characters are the

TABLE 2.—Means, standard errors (in parentheses), and ranges for morphological characters of the 1977 brood year hatchery samples of juvenile coho salmon and the hatchery water incubation temperatures for the first month of incubation. Sample sizes were 15. The data are listed in north to south order of the sampling location.

Stock and (in parentheses) incubation water temperatures (°C)	Scales in lateral series	Scales above lateral line	Anal rays	Gill rakers	Branchiostegals	Vertebrae
Bonneville Hatchery (5.4) (Columbia River)	133.33 (.61) 129-138	26.73 (.27) 25-29	13.93 (.12) 13-15	22.53 (.29) 21-25	27.00 (.32) 25-29	65.80 (.15) 65-67
Big Creek Hatchery (7.2)	133.60 (.46) 130-136	27.20 (.33) 26-30	13.53 (.13) 13-14	23.13 (.22) 22-25	25.60 (.24) 23-27	66.07 (.21) 65-67
Cowlitz Hatchery stock (7.2) (Big Creek Hatchery)	132.20 (.40) 129-135	26.60 (.41) 25-30	13.60 (.13) 13-14	21.80 (.22) 20-23	26.00 (.34) 24-28	65.67 (.16) 65-67
North Nehalem Hatchery (7.7)	130.93 (.42) 128-134	27.73 (.25) 26-29	13.73 (.15) 13-15	23.07 (.27) 21-24	26.13 (.29) 24-28	65.27 (.18) 64-66
Trask River Hatchery (9.9)	130.33 (.42) 128-133	25.53 (.32) 23-27	13.67 (.13) 13-14	22.73 (.23) 21-24	25.60 (.32) 24-28	65.40 (.24) 63-66
Salmon River Hatchery (7.8)	130.53 (.59) 127-135	26.80 (.28) 25-29	13.67 (.16) 13-14	22.40 (.16) 22-24	26.27 (.25) 25-29	65.53 (.19) 64-66
Fall Creek Hatchery (7.4) (Alsea River)	131.53 (.68) 127-136	26.20 (.33) 24-28	13.80 (.17) 13-15	22.53 (.27) 21-24	26.07 (.23) 25-28	66.13 (.19) 65-67
Umpqua Hatchery stock (8.6) (Smith River) Cole Rivers Hatchery	129.07 (.37) 126-131	26.40 (.32) 24-29	13.40 (.13) 13-14	21.47 (.17) 21-23	25.87 (.24) 24-28	65.40 (.13) 65-66
Cole Rivers Hatchery (8.6) (Rogue River)	130.33 (.66) 125-134	26.20 (.33) 24-28	13.80 (.17) 13-15	22.20 (.30) 20-24	26.20 (.24) 25-28	65.20 (.26) 64-67

result of selection, several interacting selective forces were involved.

Life History Characters

Earlier peak spawning times (Table 7) were strongly associated with the northern stream systems and with stream systems having large estuaries (Table 6). However, the correlation of peak spawning time with size of estuary may be biased by the large number of samples from Columbia River hatcheries: spawning times of stocks from the Columbia River are earlier than those of coastal stocks, and the Columbia River has a large estuary. Selection for earlier spawning times through hatchery practices may be the cause for the differences in spawning times between hatchery and wild stocks in the North Nehalem, Trask, and Alsea Rivers. Selection for earlier spawning times has been observed in a steelhead trout hatchery program (Millenbach 1973). At hatcheries using wild stocks as sources for eggs and sperm, peak spawning times were similar to those of naturally spawning fish in the respective stream system.

The proportion of females (Table 7) appeared to be higher in the southern stream systems, suggesting that jacks were more common there. The effective sex ratio, including jacks, at the time of spawning should be close to 1:1 (Fisher 1930). If only 3-yr-old males and females are counted, the proportion of females should be >0.50, the margin above 0.50 depending on how many jacks returned in the previous year. However, the proportion of males was higher than that of females in stocks from the Quilcene, Quinault, Sandy, North Nehalem, Nehalem, Trask, Salmon, Alsea, Umpqua, and Rogue Rivers. Nikolskii (1969) reviewed several possible causes for sex ratios departing from 1:1; however, the reason for the high proportion of males in these stocks is not known.

Isozyme Gene Frequencies

Transferrin gene frequencies (Figs. 2, 3), correlated significantly with six of the stream characters (Table 6). The best model from stepwise multiple regression explained only 68% of the variation in gene frequencies. Analysis of the relationships of the "A" allele frequencies with basin area (Fig. 4) and latitude (Fig. 5) explained the variation more simply than did the stepwise regression model. These correlations showed

TABLE 3.—Means, standard errors (in parentheses), and ranges of morphological characters for 1977 brood year samples of wild juvenile coho salmon. Sample size was 12 for all stream systems except Tenmile Lakes and Coquille River (15 each). The data are listed in north to south order of the sampling locations.

Stream system	Scales in lateral series	Scale rows above lateral core	Anal fin rays	Gill rakers	Branchiostegals	Vertebrae
North Nehalem River	132 25	27 75	13 58	23 25	26 75	65 50
	(88)	(33)	(.15)	(37)	(25)	(26)
	126-137	26-30	13-14	22-25	26-28	63-66
Nehalem River	132 50	26 67	13 75	23 00	27 33	65 75
	(77)	(35)	(13)	(25)	(22)	(25)
	127-136	25-29	13-14	22-24	26-28	64-67
Trask River	131 17	26 50	14 00	22 92	26 58	65 83
	(47)	(31)	(12)	(31)	(26)	(11)
	128-133	24-28	13-15	21-24	25-28	65-66
Nestucca River	132 17	26-83	14 00	22 92	27 25	65.58
	(68)	(40)	(12)	(34)	(28)	(19)
	128-136	25-29	13-15	21-25	26-29	65-67
Salmon River	131 83	26 92	13 67	23 08	26 67	65 00
	(61)	(31)	(14)	(29)	(19)	(17)
	128-135	24-28	13-14	22-25	26-28	64-66
Siletz River	130.33	27 08	13 58	23 00	27 50	65 25
	(61)	(29)	(15)	(21)	(23)	(28)
	128-135	26-29	13-14	22-24	26-29	63-67
Beaver Creek	132 27	27 33	13 27	23 27	27 18	65 33
	(49)	(38)	(20)	(36)	(30)	(14)
	130-135	25-29	12 14	21-25	26-29	65-66
Alsea River	131 25	27 17	13 67	23 17	26 83	65 25
	(.37)	(30)	(19)	(34)	(30)	(18)
	129-134	26-29	12-14	21-25	26-28	64-66
Umpqua River	131 75	26 83	13 25	22 92	27 00	65 83
	(70)	(40)	(13)	(19)	(28)	(27)
	128-136	25-30	13-14	22-24	26-29	65-68
Tenmile Lakes	131 73	26 20	13 47	22 53	26 60	65.73
	(58)	(28)	(13)	(19)	(31)	(25)
	128-136	25-29	13-14	21-24	25-28	64-67
Coquille River	131 67	26 27	13 27	22 40	26 47	65 93
	(43)	(43)	(18)	(19)	(27)	(21)
	129-134	24-30	13-14	21-24	24-28	65-67
Rogue River	132 75	26 58	14 00	22 50	26 92	65.42
	(59)	(26)	(17)	(31)	(.40)	(15)
	131-137	25-28	13-15	21-25	24-29	65-66

TABLE 4.—Hatchery stocks of coho salmon in which differences in morphological characters occurred between the 1976 and 1977 brood years as determined by a two-sample test.

Hatchery	Lateral series scales	Scales above lateral line	Anal rays	Gill rakers	Branchiostegal rays	Vertebrae
Cascade-Bonneville		**				**
Cowlitz stock		**			**	**
Big Creek		**	**			
Trask River	**	**				*
Salmon River					*	
Alsea River		**			*	
Umpqua River	**			*	*	

*$P<0.05$; **$P<0.01$

that the stocks from large stream systems and the southernmost stream systems had high frequencies of the "A" allele, whereas the frequencies in the smaller stream systems and northern stream systems were highly variable. Combining these two relationships helps explain the pattern of transferrin gene frequencies. Frequencies of the "A" allele were high in stocks from large stream systems regardless of latitude, and in southern stocks regardless of stream size. Stocks from smaller stream systems on the northern Oregon coast and in Washington had higher frequencies of the "C" allele.

The factors affecting the patterns of transferrin gene frequencies in coho salmon stocks are not known. However, Utter et al. (1980) suggested that the frequencies may be influenced by bacteriostatic properties associated with the different transferrin alleles. Genotypes of transferrin had differential mortality when exposed to bacterial kidney disease in studies by Suzumoto et al. (1977) and Winter et al. (1980b), and to vibriosis, cold-water disease, and furunculosis in a study by Pratschner (1978). Transferrin genotype was also related both to differences in juvenile growth rates and to propensity to return as jacks (McIntyre and Johnson 1977).

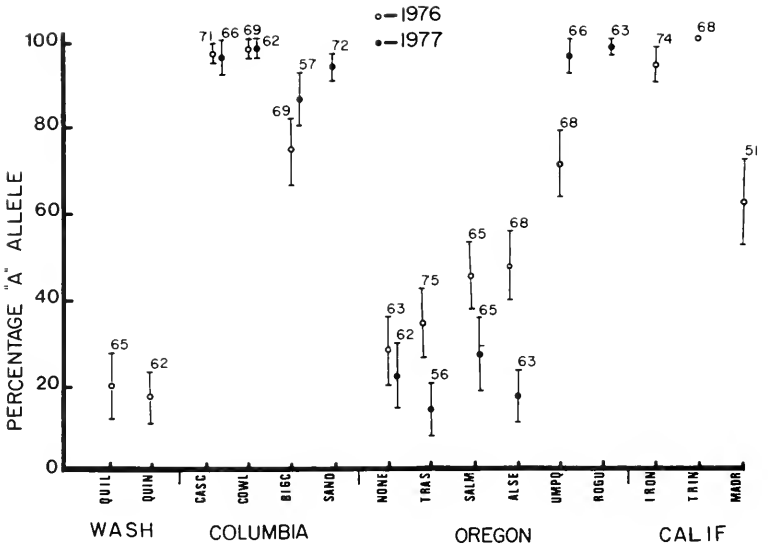

FIGURE 2.—Transferrin gene frequencies of hatchery coho salmon. Samples are arranged from north to south. Vertical lines represent 95% confidence intervals; numbers above the line show sample sizes. Location codes are as in Figure 1.

TABLE 5.—Environmental data for the stream systems sampled in this study.

Stream system	Spawning distance (km)	Latitude	Estuary area (ha)	Estuary length (km)	Gradient (m/km)	Runoff in spring	Basin area (km²)
Washington							
Quilcene River	13	47 75	[1]512	3 2	19 2	yes	[2]179
Quinault River	92	47.33	[1]64	3 2	2 8	yes	[2]1,123
Oregon							
Columbia River							
Cascade-Bonneville Hatcheries	235	46 25	[1]37,513	236.5	0	yes	[3]51,769
Cowlitz Hatchery stock	193	46 25	[1]37,513	109 4	0 8	yes	[2]6,418
Big Creek Hatchery	60	46.25	[1]37,513	43 4	14 2	no	[2]88
Sandy River Hatchery	270	46 25	[1]37,513	194 7	7.1	yes	[2]1,299
North Nehalem River	45	46 25	[4]1,128	11.3	8 6	no	[1]233
Nehalem River	195	45.68	[4]1,128	24 1	2.4	no	[2]2,192
Trask River	72	45.52	[4]3,480	20.9	9.5	no	[5]455
Nestucca River	76	45.16	[4]400	12 9	7.7	no	[2]657
Salmon River	29	45.05	[4]82	6.4	13.0	no	[6]194
Siletz River	122	44.93	[4]475	37 0	3 4	no	[2]797
Beaver Creek	21	44.52	[1]3	3.2	4.3	no	[1]31
Alsea River	93	44 43	[4]858	19 3	3 2	no	[6]1,227
Umpqua River	372	43 68	[4]2,285	45 0	1.9	yes	[6]11,801
Smith River[7]	122	43.68	[4]2,285	24 1	2 5	no	[2]898
Tenmile Lakes	24	43.57	[1]1	1 6	3.2	no	[5]254
Coquille River	138	43 11	[4]308	66 0	3.4	no	[6]2,738
Rogue River	249	42.44	[4]251	6.4	1.9	yes	[6]13,199
California							
Klamath River	293	41.58	[1]200	3 2	2 2	yes	[8]31,314
Trinity River	235	41.58	[1]200	3.2	2.4	yes	[8]7,383
Mad River	72	40.95	[1]200	6 4	6 5	no	[8]1,255

[1]Provided by district biologists
[2]Pacific Northwest River Basins Commission 1966, 1967, 1968, 1969, 1972 River Mile Indices. Hydrol Hydraul. Comm.
[3]Personal estimate of area utilized by coho in the Columbia drainage.
[4]Gaumer, T., D. Demory, and L. Osis 1973 Estuary resources use study Fish Comm Oreg , Div Manage Res
[5]Water Resources Board of Oregon. 1969 Oregon long range requirements for water Salem, Oreg , 397 p.
[6]Wilsey and Ham Incorp. 1974 Estuarine resources of the Oregon coast A natural resource inventory report to the Oregon Coastal Conservation and Development Commission, Portland, Oreg , 233 p
[7]Source of Umpqua Hatchery stock
[8]United States Geological Survey 1977 Water resources data for California water year 1977 Water Data Rep CA 77-2.

Therefore, diseases, life history characteristics, and other factors may play a role in maintaining the patterns of transferrin gene frequencies.

Transferrin gene frequencies were in good agreement between the two year classes of Oregon coast wild stocks, despite the small size of some of the samples (Fig. 3). The heterogeneity between year classes was greater for the Oregon

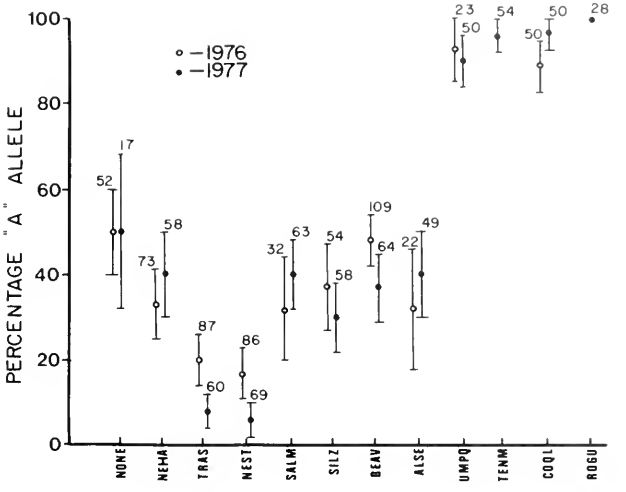

FIGURE 3.—Transferrin gene frequencies of wild coho salmon stocks for 1976 and 1977 brood years. Stocks are arranged from north to south. Bars represent 95% confidence intervals and the sample sizes are above the bars. Location codes are as in Figure 1.

TABLE 6.—Statistically significant correlation coefficients between the characteristics of the coho salmon stocks and the environmental characteristics of their respective stream systems. $r = 0.28$ at $\alpha = 0.05$ and 0.37 at $\alpha = 0.01$.

Characteristics		
Stock	Environmental	Correlation
Scales in lateral series	Spawning distance	0.418
	Estuary size	0.341
	Estuary length	0.430
	Gradient	−0.368
Scale rows	Latitude	0.360
	Spring runoff	0.315
Anal rays	Estuary size	0.414
	Latitude	0.382
Gill rakers	Latitude	0.346
	Basin area	−0.353
	Spring runoff	−0.319
Branchiostegals	Latitude	0.431
	Spring runoff	0.381
Vertebrae	Estuary size	0.350
	Basin area	0.445
	Gradient	−0.432
	Spawning distance	0.549
	Estuary length	0.533
Proportion of females	Latitude	−0.426
Time of peak spawning	Estuary size	−0.613
	Spring runoff	−0.345
	Estuary length	−0.391
	Latitude	−0.702
Phosphoglucose isomerase	Spring runoff	−0.410
Transferrin	Estuary length	0.326
	Latitude	−0.381
	Spawning distance	0.590
	Basin area	0.588
	Spring runoff	0.528
	Gradient	−0.596

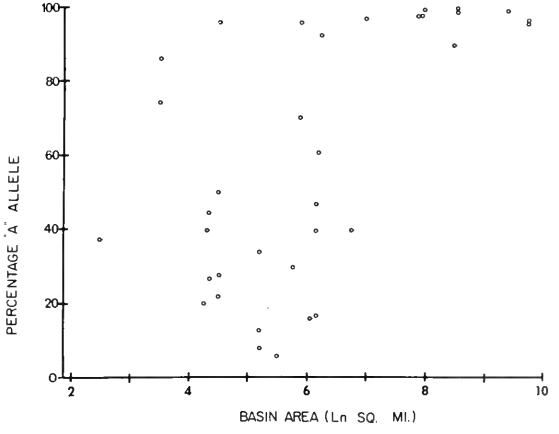

FIGURE 4.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by basin area, in ln square miles.

coast hatchery stocks (Fig. 2). The gene frequencies of hatchery stocks may have been altered by earlier importing of stocks with different gene frequencies, or by disease epizootics. If fish with certain transferrin genotypes have different resistances to diseases, and if epizootics are more severe because of the higher densities of fish in hatcheries, then the transferrin gene frequency of a given year class could be altered without affecting the other two year classes.

The phosphoglucose isomerase variant (Table 7) was present only in samples from Oregon stocks—particularly those from the northern Oregon coast. May (1975) reported this variant in Washington stocks.

Similarity of Stocks

The groups of stocks of coho salmon found to be most similar by the agglomerative cluster analysis (Fig. 6) were composed of northern

TABLE 7.—Proportion of females, time of peak spawning, and gene frequency, 95% confidence interval (CI), and sample size of phosphoglucose isomerase variant of wild and hatchery stocks of coho salmon. Years of data used to estimate proportion of females are in parentheses. The data are listed in north to south order of the sampling locations.

Stream system	Proportion of females[1]	Years	Time of peak spawing[1]	Proportion of females	Years	Time of peak spawning[1]	1977			1976			1977		
							Frequency	95% CI	Sample size	Frequency	95% CI	Sample size	Frequency	95% CI	Sample size
Washington															
Quilcene Hatchery				0.41	1972-78	Oct 15-30				0	—	36			
Quinault Hatchery				0 37	1973-75	Oct 15-30				0	—	40			
Oregon															
Columbia River					—										
Cascade-Bonneville Hatchery				0 51	1970,72-76	Nov 1 -15				0	—	40	0	—	60
Cowlitz Hatchery stock				0.50	([2])	Nov.1 -15				0	—	40	0	—	60
Big Creek Hatchery				0.55	1970-76	Nov 1 -15				0	—	40	0	—	40
Sandy River Hatchery				0 45	1970-76	Nov 1 -15				0	—	40			
North Nehalem River	0 43	([3])	Dec 1 -15	0 43	1970-76	Nov 1 -15	0 05	0 08	19	0 05	0 04	44	0 08	0 04	60
Nehalem River	0 43	1949-69	Dec.1 -15				0 11	0 06	64						
Trask River	0 33	1949-69	Dec 1 -15	0 43	1970-76	Nov 1 -15	0 06	0 04	62	0 08	0.06	40	0 20	0 08	60
Nestucca River	0 56	1949-69	Dec.1 -15				0 03	0 04	59						
Salmon River	0 46	1975-77	Dec 1 -15	0 46	1975-77	Dec 1 -15	0 01	0 02	64	0	—	40	0	—	60
Siletz River	0 54	1949-69	Dec 1 -15												
Beaver Creek	0 58	1949-69	Dec 15-31				0	—	32						
Alsea River	0 53	1949-69	Dec.1 -15	0 42	1970-76	Nov 16-30	0.01	0 02	49	0 05	0 04	40	0 15	0 06	60
Umpqua River	0 63	1949-69	Dec.1 -15	0 49	1977-78	Dec 1 -15	0	—	41	0	—	40	0		60
Tenmile Lake	0 65	[4]1954-74	Dec 15-31				0	—	50						
Coquille River	0 55	1949-69	Dec 1 -15				0.01	—	59						
Rogue River	0 44	([3])	Dec.1 -15	0 44	1974,75, 77 & 78	Dec 1 -15	0	—	29				0		60
California															
Klamath River															
Irongate Hatchery				0 53	1969-78	Dec 1 -15				0		40			
Trinity Hatchery				0.53	1966-78	Dec 1 -15				0		40			
Mad River				0 62	1971-78	Dec 1 -15				0		36			

[1]Three-year-old fish only
[2]Estimated by hatchery manager
[3]Estimated from hatchery data
[4]Except 1959

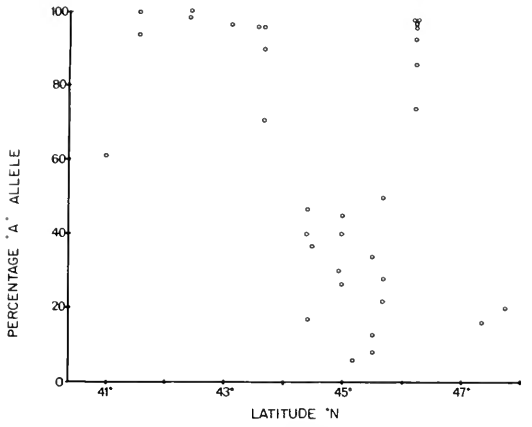

FIGURE 5.—Transferrin gene frequencies for wild and hatchery coho salmon stocks arranged by latitudes.

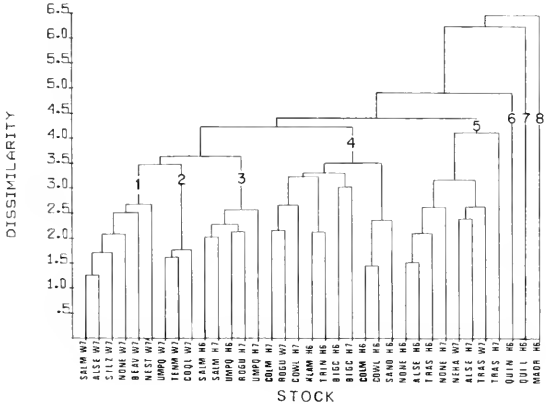

FIGURE 6.—Dendrogram of the agglomerative cluster analysis for all stocks of wild and hatchery coho salmon of two brood years, 1976 and 1977. Euclidean distance was the dissimilarity measure and group average was the clustering strategy. Location codes are as in Figure 1. The other codes are as follows: H6, hatchery stock of the 1976 brood year; H7, hatchery stock of the 1977 brood year; and W7, wild stock from the 1977 brood year.

Oregon coast wild stocks (cluster 1), southern Oregon coast wild stocks (cluster 2), stocks from hatcheries that used wild stocks for the egg source (cluster 3), stocks from large river systems (cluster 4), hatchery stocks and two wild stocks from the northern Oregon coast (cluster 5), and three individual hatchery stocks from California and Washington (clusters 6-8).

Canonical variate analysis on the five larger clusters produced three canonical variables that were significant ($\alpha = 0.05$). When these three variables were plotted against each other, only clusters 1 and 5 (consisting of wild stocks and hatchery stocks, both from the northern Oregon coast) were not completely separate in three-dimensional space. The other three clusters were discrete, suggesting that intercluster differences were stronger than between clusters 1 and 5. Statistical testing for differences between the clusters would not be valid because the necessary assumption of randomness of data is violated.

The results of the canonical variate analysis must be interpreted with caution because the variation within each cluster was reduced by our using the averages of the morphological characters. This reduction of variation facilitates discrimination between clusters by canonical variate analysis, so that quantitative comparisons of cluster discreteness cannot be made. Individual phenotypes undoubtedly overlap between stocks or between clusters; however, the multivariate analysis of variance did indicate that significant differences existed among the stocks for each of the morphological characters. We characterized the stocks by the average phenotypes in order to estimate the phenotypes typical for each stream system, and on that basis the results of the canonical variate analysis suggested that there were discrete differences between all clusters except 1 and 5.

The results of the agglomerative and divisive cluster analyses were similar. At the 13-cluster level of the divisive analysis (Table 8), all but two clusters were identical with clusters from the agglomerative cluster analysis dendrogram. The results of these analyses should be interpreted cautiously, because they are based on only 10 characteristics—a small number compared with the total number of genetically related characteristics possible. If other characteristics had been used, the results might have differed. Thus, we did not emphasize the exact order or the levels of dissimilarity at which any two clusters joined together; rather, we observed only general trends in the clustering patterns.

Three general trends are apparent in the clustering patterns of the agglomerative cluster analysis dendrogram. First, the stocks from the larger stream systems (Columbia, Rogue, and Klamath Rivers) were more similar to each other than to the stocks from smaller streams. The only exceptions to this trend were wild stock from the Umpqua River and the Umpqua and Rogue hatchery stocks. The Umpqua wild stock was

TABLE 8.—Coho salmon stocks at the 13 cluster level of the divisive cluster analysis. "Wild" denotes wild stocks.

Cluster no.	Divisive cluster analysis stock	Brood year
1	Cascade Hatchery	1976
	Cowlitz Hatchery	1976
	Sandy Hatchery	1976
2	Salmon River Hatchery	1976, 1977
	Rogue River Hatchery	1977
	Umpqua River Hatchery	1976, 1977
3	North Nehalem wild	1977
	Nestucca River wild	1977
	Salmon River wild	1977
	Siletz River wild	1977
	Beaver Creek wild	1977
	Alsea River wild	1977
4	Quilcene Hatchery	1976
5	Nehalem River wild	1977
	Trask River wild	1977
6	Mad River Hatchery	1976
7	North Nehalem Hatchery	1976, 1977
	Trask Hatchery	1976
	Alsea Hatchery	1976
8	Umpqua River wild	1977
	Tenmile Lake wild	1977
	Coquille River wild	1977
9	Trask Hatchery	1977
	Alsea Hatchery	1977
10	Quinault Hatchery	1977
11	Bonneville Hatchery	1977
	Cowlitz Hatchery	1977
	Rogue wild stock	1977
12	Irongate Hatchery	1976
	Trinity Hatchery	1976
13	Big Creek Hatchery	1976, 1977

associated with the other southern Oregon coast wild stocks, and the Rogue and Umpqua hatchery stocks were in the cluster with other hatcheries that used wild stocks as egg sources.

The second trend observed in the dendrogram was geographical clustering. Three stocks from Washington and California were dissimilar to the Oregon stocks, and the Oregon wild stocks clustered into two groups, northern and southern coastal stocks.

The third trend in the dendrogram was for hatchery and wild stocks to cluster independently. One of the clusters was composed entirely of wild stocks from the northern Oregon coast, and another included all but one of the northern Oregon coast hatchery stocks, in addition to two wild stocks from the northern Oregon coast. The hatchery stock excluded from this cluster (no. 5) was from the Salmon River, a stock developed from eggs of wild coho salmon; both brood years of this stock were in the cluster of hatcheries that used wild stocks as an egg source. The rest of the northern Oregon coast hatcheries used returning hatchery-reared adults for egg sources. The two wild stocks in this cluster were from the Trask and Nehalem Rivers. They are also similar to the other wild stocks; however, because of the mechanics of the group-average clustering strategy, they both clustered first with the hatchery stocks. The average Euclidean distance between the Nehalem wild stock and the other wild stocks was less than that between the Nehalem wild stock and the hatchery stocks of cluster 5. The close relationships of the stocks in clusters 1 and 5 were also apparent in the results of the canonical variate analysis, which showed these two clusters to be continuous.

The three trends in the clustering pattern indicated that coho salmon stocks from similar environments had similar phenotypes. These trends provide some guidance for the transfer of coho salmon stocks. Geographical clustering indicates that the phenotypic or perhaps genetic similarity between stocks probably decreases as the distance between stocks increases. McIntyre[8] showed a strong negative correlation for the distance between stream systems and the genetic similarity of the steelhead trout stocks in those stream systems. If a similar relation between phenotype and distance exists among coho salmon stocks, survival rate would be expected to vary inversely with the distance that the stock is transferred from its native stream. The crucial question from the management standpoint, assuming the relationships we found are real, is how far stocks can be transferred before decreasing survival rate and the increasing genetic impact on the native stocks reduce the practicality of such transfers.

Although geographical distance can be an important factor in selecting a donor stock, other considerations must also be taken into account. The difference between stocks from large and small stream systems illustrates a problem in basing stock transfers primarily on geographical distance. Stocks from large stream systems were more similar to stocks in distant large systems than to stocks in small stream systems that were geographically close. Other environmental variables may also differ, affecting the phenotypes of geographically close stocks. Characteristics such as time of peak spawning or transferrin genotype may be closely related to flow and temperature regimes or to disease organisms present in the stream systems. These characteristics and others not included in this

[8]McIntyre, J. D. 1976. The report of interbreeding of artificially propagated and native stocks of steelhead trout. Oreg. Dep. Fish Wildl., Res. Sect., Steelhead Annu. Rep., 22 p.

study all should play a role in choosing stocks for transfer to other stream systems.

The third trend mentioned (that of hatchery and wild stocks diverging toward different phenotypes) presents a problem to managers who must choose the best stock for transfer to other stream systems. The separate clustering of hatchery and wild stocks suggests that hatchery stocks have become dissimilar to wild stocks—even those that inhabit the same drainage. Studies with steelhead trout indicated that hatchery fish survived better in hatchery ponds, whereas wild fish had higher survival in streams (Reisenbichler and McIntyre 1977). The dissimilarity between hatchery and wild stocks may play a role in reducing the survival of hatchery-reared coho salmon when they are released into a stream system.

Similarity of Stream Systems and Wild Stocks

Because coho salmon appear to have similar phenotypes in similar environments, one could possibly relate phenotypes of stocks with descriptions of their stream basins (Tables 5, 9). However, comparisons of an agglomerative cluster analysis of wild stocks (Fig. 7) with a cluster analysis of stream characters (Fig. 8) indicated that they were less similar than we had anticipated—although we expected some differences because the stream characters were not necessarily related to taxonomic characters used in this study.

CONCLUSIONS

Individual characters of the stocks examined by us showed a variety of responses to stream characters. Time of peak spawning was strongly correlated with latitude, whereas other characters were significantly correlated with several environmental gradients, suggesting that interactions determining stock phenotypes are complex. The variability of the stock character may also change along environmental gradients, as demonstrated by the transferrin genotype (Figs. 4, 5).

The results of the cluster analysis indicate that stocks that are geographically close are similar, that stocks from large stream systems are similar to each other, that stocks from coastal stream systems are similar to each other, and that hatch-

TABLE 9.—Fish species and myxosporidan parasite, *Ceratamyxa shasta*, present in the Oregon stream systems. X = present.

Stream systems	Carp	Oregon chub	Squawfish	Redside shiner	*Catostomus* sp.	Speckled dace	Striped bass	Brown bullhead	Largemouth bass	*Ceratamyxa shasta*
Nehalem River					X				X	X
Trask River										
Nestucca River						X				
Salmon River										
Siletz River						X		X		
Beaver Creek						X				
Alsea River						X				
Smith River		X	X	X	X		X	X		
Umpqua River		X	X	X	X	X	X	X		
Tenmile Lake						X		X	X	
Coquille River					X	X	X	X		
Rogue River	X			X	X		X	X		X

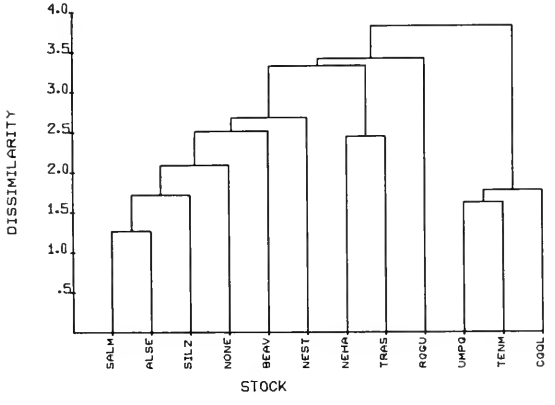

FIGURE 7.—Dendrogram of the agglomerative cluster analysis for wild coho salmon stocks with a Euclidean distance dissimilarity measure and group average clustering strategy. Location codes are as in Figure 1.

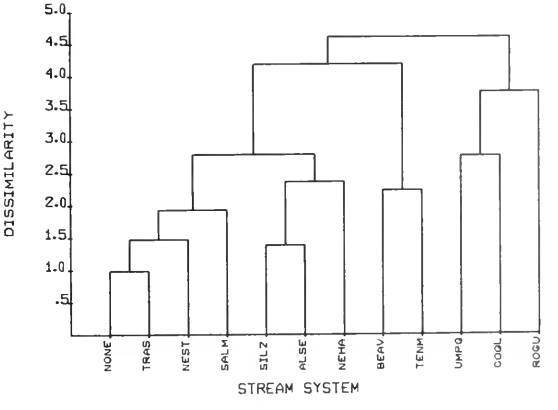

FIGURE 8.—Dendrogram of the agglomerative cluster analysis for stream systems with a Euclidean distance measure and group average clustering strategy. Location codes are as in Figure 1.

ery and wild stocks are dissimilar. In general, coho salmon stocks from similar environments appear to have similar phenotypes; however, groupings obtained from cluster analyses of coho salmon stocks and corresponding stream systems were dissimilar. This dissimilarity may be a result of our using only a small number of characters for analysis. As additional characters are considered, additional trends may become evident. The characters in this study, in concert with other characters, should be used in future evaluations of genetic similarities between stocks for an eventual characterization of stocks that will ensure effective transplantation.

In addition to providing information which may be useful for selecting donor stocks for hatchery programs, the results of this study also suggest a potential weakness in hatchery supplementation. Selection through hatchery environment and hatchery practices may be changing the overall phenotype of hatchery stocks, as well as the between-year variability of individual genotypes (as we found for transferrin). If these changes result in reduced performance of the donor stocks in other stream systems, practices designed to increase hatchery production must be weighed against the actual benefits to wild production.

We believe that this study demonstrates a relationship between phenotypic characters and certain habitat types. The differences in phenotype that are attributable to hatchery or wild origin, geographic proximity, and small or large stream systems may provide a first basis for judging the advisability of stock transfers.

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We express our appreciation to Carl Bond for his suggestions concerning the morphological characters, to Norbert Hartmann for his advice concerning the analysis of the data, to Fred Utter for taking the time to share his knowledge of electrophoresis, and to Al McGie for providing data on the proportion of females on spawning ground surveys. Funds for this project were provided by the Oregon Department of Fish and Wildlife.

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REPRODUCTIVE BIOLOGY OF WESTERN ATLANTIC BLUEFIN TUNA[1]

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ABSTRACT

Ovaries of bluefin tuna, *Thunnus thynnus*, were collected from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight of the western North Atlantic, and off the northeast coast of the United States. There was relatively little development towards maturity in age 1 through age 7 fish from the Middle Atlantic Bight as evidenced by low gonosomatic index values and histological examination of ovaries. Well-developed ovaries were present in giant bluefin tuna from the Gulf of Mexico and Florida Straits, with heaviest spawning occurring in May. For bluefin tuna measuring 205-269 cm fork length and 156-324 kg round weight, the average number of eggs measuring 0.33 mm in diameter and larger was estimated at 60.3 million, and the average number of eggs measuring 0.47 mm in diameter and larger was estimated at 34.2 million.

Atlantic bluefin tuna, *Thunnus thynnus*, are seasonally distributed over most of the North Atlantic. They are found from Newfoundland to Brazil and from Norway to the Canary Islands (Gibbs and Collette 1967).

In the western Atlantic, a sport fishery for bluefin tuna exists off the east coast of the United States from Maine through North Carolina and along the western Bahamas and the eastern coast of Canada. Also, a substantial commercial bluefin tuna fishery exists in the western Atlantic. There is purse seining along the east coast of the United States from Massachusetts to North Carolina and a handline and harpoon fishery off Massachusetts and Maine. A substantial Japanese longline fishery is present off the east coast of the United States and in the Gulf of Mexico.

In the eastern Atlantic, a sport fishery for bluefin tuna exists around the Canary Islands and a substantial commercial fishery occurs off Europe and North Africa. Purse seining is conducted off the Atlantic coast of Norway and Morocco, the Mediterranean coast of France, the Adriatic coast of Italy and Yugoslavia, in the Tyrrhenian Sea off Italy, and occasionally in the North Sea off Denmark. An important hook-and-line bait fishery occurs in the Bay of Biscay off France and Spain, off Morocco, the Azores, the Canary Islands, the Mediterranean coast of Spain, and occasionally off Turkey. Trap fisheries were present off southern Portugal, southern Spain, and the Straits of Gibraltar, as well as along the Mediterranean coast of Morocco, Tunisia, and Sicily. There is a significant Japanese longline bluefin tuna fishery in the Mediterranean Sea, Bay of Biscay, and off western Europe.

There has been a substantial reduction in the Atlantic-wide catch of bluefin tuna from 38,500 t in 1964 to 12,500 t in 1973 with no large reductions in effort (Miyake et al[3].) A number of studies have been made, and are continuing, to understand the reason for this decline (Parks 1977; Shingu and Hisada 1980; Parrack 1980). Of the various aspects of the dynamics of fish populations, the measure of reproductive potential is of primary importance since it is a basic determinant of productivity. It is used to separate subpopulations, to estimate mortality, and, with ichthyoplankton data, to estimate stock size.

Two major bluefin tuna spawning areas are located in the Atlantic approximately 4,000 mi apart: In the Gulf of Mexico (Richards 1976; Montolio and Juarez 1977; Rivas 1978) and the Florida Straits (Rivas 1954; Baglin 1976) during April, May, and June; and in the Mediterranean Sea during May, June, and July (Frade and Manaças 1933; Rodríguez-Roda 1964). Al-

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[3]Miyake, M. P., A. De Boisset, and S. Manning (compilers). 1974. Int. Comm. Conserv. Atl. Tunas, Stat. Bull. 5. Unnumbered pages.

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though these two spawning grounds have been well documented, a question remains whether bluefin tuna spawn elsewhere and at other times. Mather[4] believes that some bluefin tuna probably spawn in late spring near the northern edge of the Gulf Stream off the eastern United States. Berrien et al. (1978) have reported collecting bluefin tuna larvae from this area during April and June 1966. These larvae, however, could have drifted to this area from spawning grounds farther south.

In this paper, I describe bluefin tuna ovaries from the Middle Atlantic Bight (the U.S. coastal area between Cape Cod and Cape Hatteras) and examine the possibility that this may be another significant spawning area for bluefin tuna. Also, I make some comparisons of female gonadal development between the known spawning areas.

My literature review on bluefin tuna shows there is a need for additional information on the bluefin tuna's reproductive potential. A wide range in fecundity estimates was found. Frade (1950) reported that an eastern Atlantic 160 kg bluefin tuna produced 18.7 million eggs. Williamson (1962) stated that the ovaries of a 272.4 kg western Atlantic bluefin tuna contained about 1.0 million eggs. Rodríguez-Roda (1967) estimated that off southern Spain a 54 kg fish could produce 5.5 million eggs and a 235 kg bluefin tuna could produce over 30.0 million eggs. Baglin (1976) estimated that a 188.4 kg western Atlantic bluefin tuna could produce 16.7 million eggs and that a 271.5 kg bluefin tuna could produce 31.4 million eggs. Baglin and Rivas (1977) indicated that a 324 kg western Atlantic tuna could produce 57.6 million eggs. I determined the fecundity of bluefin tuna taken from the United States sport fishery in the Florida Straits and Gulf of Mexico and from the Japanese longline fishery in the Gulf of Mexico and compared my findings with previous estimates. I have also examined monthly sex ratios for western Atlantic bluefin tuna.

MATERIALS AND METHODS

Bluefin tuna from the Gulf of Mexico, Florida Straits, Middle Atlantic Bight, and off the northeast coast of the United States were sampled from anglers' catches. Bluefin tuna samples from purse seine catches came from the Middle Atlantic Bight and the northeast coast of the United States. Bluefin tuna were also sampled from the Japanese longline fishery in the Gulf of Mexico and from the New England handgear fishery.

Throughout this paper the classification system of Rivas (1979) was used. Thus, small bluefin tuna are 50-129 cm fork length (FL) and 3-44 kg round weight, medium bluefin tuna are 130-180 cm FL and 45-130 kg round weight, and giant bluefin tuna are >180 cm FL and >130 kg round weight.

Sex data were obtained from 283 small and medium bluefin tuna captured by commercial and sport fishermen off the Middle Atlantic Bight (1974-77). Also, sex data were obtained from 3,429 giant bluefin tuna captured by sport and commercial fishermen in the Gulf of Mexico and along the northeast coast of the United States from North Carolina to Maine, and from fish taken by sport fishermen in the Bahamas (1975-78).

Straight fork length (cm) was measured with calipers and round weight was recorded in pounds and later converted to kilograms. In some instances where either weight or length was unknown, a functional regression (Baglin 1980) was used for estimating the missing measurement.

Small and medium fish were assigned an age based on a length-weight-age conversion table presented by Coan (1976). No ages were assigned to giant fish because of the difficulty experienced in aging them accurately.

Ovaries were examined from 81 small and medium bluefin tuna caught from 1974 through 1977 and from 403 giant bluefin tuna collected during 1965 through 1968 and 1974 through 1978. Ovaries were stored in 10% Formalin[5] and later blotted dry and weighed in grams. The gonosomatic index (GSI) (ovary weight as a percentage of total body weight) was used as a gross indicator of maturity. Only fork length was taken from Japanese longline samples from the Gulf of Mexico for which the GSI was calculated using an estimated body weight from the length-weight relationship of Baglin (1980).

A detailed examination of ovaries from 292

[4]Mather, F. J., III. 1973. The bluefin tuna situation. Proc. 16th Annu. Int. Game Fish. Res. Conf., p. 93-120.

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

fish was conducted using histological techniques. Ovaries were sectioned at 8 μ and stained either with haematoxylin and eosin or trichrome stain. The oocytes were grouped into stages according to the classification system of Kraft and Peters (1963) and Smith (1965). From each prepared slide, a measurement was taken of the largest egg diameter. The egg diameters were measured with an ocular micrometer at 30 × magnification, and the orientation of egg diameters was assumed to be random. Stage of maturity was thus based on the histological examinations.

A test was made for heterogeneity of egg size within the ovary. Thin cross sections were taken from the anterior, middle, and posterior parts of one ovary of a mature fish and each section was subdivided into three subsamples, representing the center, midregion, and periphery of the ovary (Otsu and Uchida 1959). Egg diameters from each area were then measured and compared statistically.

Fecundity, defined as the potential number of mature eggs (yolked ova) that could be spawned during one reproductive season, was estimated by using a dry weight method. This consisted of taking samples from the anterior, middle, and posterior parts of each ovary. The eggs from each of these sections and from the remainder of the ovaries were then separated from the ovarian tissue by straining them over a wire screen under running water. The egg samples from each section, in an aqueous solution, were stirred and a subsample from each was pipetted into a beaker. These eggs were stirred and approximately 1-2 g wet weight were taken to be used for the fecundity estimate. The yolked eggs, which were counted and fecundity estimated, were divided into two size categories. Eggs 0.46 mm and larger that were counted were well developed and fully yolked. A second size category for which eggs were counted included smaller eggs (0.32 mm in diameter) that were not in quite as advanced stage of development, but that could possibly undergo further development and be spawned during one reproductive season. The subsample was then weighed to the nearest 0.1 mg, and the weight of the remaining eggs was recorded in grams. Fecundity estimates, rounded to the nearest 0.1 million eggs, were calculated from the relationship $C = (AD/B) + A$, where A is the number of mature ova in the subsample, B is the weight of the ova in the subsample, C is the number of mature ova, and D is the weight of ova from both ovaries minus the weight of the subsample.

RESULTS AND DISCUSSION

Sex Composition

From 1974 through 1977, sex was determined for 283 small and medium bluefin tuna from the Middle Atlantic Bight during June, July, and August (Table 1). No significant difference from an expected 1:1 sex ratio was found. Sampling for the remaining months was inadequate.

From 1975 through 1978, sex was determined for 3,429 giant bluefin tuna from the Gulf of Mexico, March through June; Bahamas, April through June; and from the northeast coast of the United States, July through October (Table 1). The deviation from an expected 1:1 sex ratio was significant for April, May, July, and August. Females were more prevalent than males in spawning aggregations during April and May. Males were more prevalent in feeding schools during July and August. No significant difference from an expected 1:1 sex ratio was found for March, June, September, and October. Sampling during the remaining months was inadequate. These findings suggest that some giant bluefin tuna segregate into distinct areal groups according to the predominating sex and that sex ratios may change with season.

TABLE 1.—Monthly sex ratios for small and medium (1974-77) and giant (1975-78) western Atlantic bluefin tuna.

Size category	Month	Number	Sex ratio males/females
Small and medium	June	204	1.02
	July	35	0.84
	August	44	1.10
Giant	March	66	1.00
	April	292	[1]0.75
	May	356	[1]0.63
	June	106	0 93
	July	800	[1]1 46
	August	1,049	[1]1.74
	September	694	0.93
	October	66	1.13

[1]Significant departure from null hypothesis at 0.05 level (chi-square).

Gonosomatic Index, Gross Morphology, and Size of Ova

The external appearance alone of tuna ovaries is inadequate for gross classification of maturity stage (Buñag 1956). The GSI (also called gonad index, maturity index, gonadosomic or gonadal-

somatic index), along with egg diameter measurements, has been a successfully used criterion for selecting specimens for fecundity studies and for determining the spawning periods for various species of fish (Vladykov 1956; Peterson 1961; Erdman, 1968; Mathur and Ramsey 1974; Baglin 1979).

On the basis of the GSI and the gross morphology and size of ova from the preserved ovaries, western Atlantic female bluefin tuna may be assigned to one of the following developmental stages:

I. Immature—Ovaries are thin, hollow tubes; nearly spherical, transparent oocytes range from 0.03 to 0.13 mm in diameter (these eggs were stained with acetocarmine to facilitate measuring). These oocytes were also present during all other developmental stages, and there was no sign of previous spawning. GSI ranges from 0.1 to 0.3.

II. Maturing—Ovaries are flaccid, opaque ova up to about 0.63 mm in diameter. GSI ranges from 0.4 to 1.9.

III. Mature—Ovaries are firm and full of eggs, with many yellow-orange ova up to 0.85 mm in diameter. GSI ranges from 2.0 to 5.3.

IV. Ripe—None of the fish studied were found to be in this developmental stage. However, a few transparent ripe eggs were found in an individual classified as Stage III. The largest of these eggs was 1.16 mm in diameter with an oil droplet 0.30 mm in diameter. This egg corresponds to Stage V of Rodríguez-Roda (1967). A fish would be classified as being ripe only when a substantial number of eggs of this size are present.

V. Spent—Ovaries are flaccid; completely spent fish had a few degenerating eggs up to 0.63 mm in diameter. Fish in this stage taken in the summer and early fall months had ovaries with a large amount of fatty tissue. GSI >0.2 but <2.0.

Size and reproductive data by estimated age and month are presented in Table 2 for 81 small and medium female bluefin tuna from the Middle Atlantic Bight of the western Atlantic and for 15 small and medium eastern Atlantic female bluefin tuna collected by Rodríguez-Roda (1967) and by Cort et al. (1976). Relatively

TABLE 2.—Length, weight, and gonadal data for 81 small and medium female western Atlantic bluefin tuna collected during 1974-77 and for 15 small and medium female eastern Atlantic bluefin collected during 1963 by Rodríguez-Roda (1967) and during 1976 by Cort et al. (1976).

		Fork length (cm)			Round weight (kg)			Ovary weight (g)			Gonosomatic index (%)			
Age	Month	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	Number
							Western Atlantic							
3	June	100	0.59	97-102	19.6	0.57	16.3-23.2	25	3.9	5-52	0.1	0.02	0.03-0.28	12
	July	96		95-100	18.7		16.8-21.8	16		10-23	0.1		0.06-0.14	6
	August	101		98-105	20.7		18.8-22.2	18		8-51	0.1		0.03-0.23	6
4	June	108		107-109	25.4		24.5-26.3	15		10-20	0.1		0.04-0.08	2
	July	121		118-122	34.2		26.8-38.1	76		68-80	0.2		0.21-0.26	3
	August	115		106-124	29.5		19.1-40.9	49		17-94	0.2		0.09-0.26	4
5	June	133	1.42	126-138	44.1	1.18	36.3-49.9	97	9.5	44-148	0.2		0.11-0.33	12
	July	133		126-140	47.2		43.6-50.8	190		149-231	0.4		0.29-0.53	2
	August	129		126-131	41.0		37.9-45.4	69		40-119	0.2		0.11-0.26	4
6	June	150	1.44	142-157	59.1	2.34	45.4-75.4	204	18.5	102-222	0.4	0.03	0.17-0.51	12
	August	150			58.1			126			0.2			1
7	June	163	0.90	157-169	80.2	2.53	65.4-91.7	434	97.9	175-1,605	0.5	0.10	0.17-1.75	14
	July	160		158-165	60.3		53.1-68.1	142		62-211	0.2		0.13-0.31	3
							Eastern Atlantic							
4	July	111			[1]26.2			150			0.6			1
5	May	130			54.0			740			1.4			1
	June	125			[1]37.0			500			1.4			1
	July	126			[1]37.8			450			1.2			1
	August	134			48.0			460			1.0			1
6	June	149			[1]61.7			900			1.5			1
	July	148			[1]61.0			860			1.4			3
	August	152			63.5			470			0.7			2
7	June	171			110.0			1,920			1.9			1
8	May	180			113.0			2,500			2.2			1
	August	185			106.0			660			0.6			2

[1]Round weight estimated using functional regression of Baglin (1980).

little development towards maturity was evident in the age 1 through age 7 western Atlantic fish with the exception of one age 7 fish collected in June with a GSI of 1.75. The eastern Atlantic small and medium fish, on the average, have a larger mean GSI than the western Atlantic small and medium fish. The largest GSI (2.2) calculated from the eastern Atlantic small- and medium-sized bluefin tuna was found for a fish captured during May at an estimated age of 8 yr.

Body and ovary size, by month, for 403 western and 75 eastern Atlantic female giant bluefin tuna are presented in Table 3, with the calculated monthly GSI presented in Figures 1 and 2. The average body and ovary size of the female giant fish from the western Atlantic was larger than that of the eastern Atlantic fish for each month. Well-developed ovaries were present in western Atlantic giant bluefin tuna during April and May. These fish were collected from the Gulf of Mexico longline and sport fishery and from the Florida Straits sport fishery. Ovarian development was minimal during October, as indicated by a low mean GSI,

TABLE 3.—Length, weight, and gonadal data for 403 female giant western Atlantic bluefin tuna collected during 1965-68, 1974-78, and for 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967).

Month	Fork length (cm)			Round weight (kg)			Ovary weight (g)			Number
	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	$\bar{X}$	SE	Range	
					Western Atlantic					
March	237	3.5	199-256	245	10.2	143-307	2,849	448	331-6,810	25
April	242	2.7	190-264	262	8.1	117-335	8,380	564	409-13,166	41
May	240	1.4	205-269	244	4.8	156-324	7,708	475	900-14,960	73
June	246	1.7	213-270	262	5.8	159-351	5,023	341	950-13,600	68
July	254	1.0	218-272	295	3.3	205-375	1,927	89	600-7,000	96
August	257	1.3	224-282	320	4.4	213-424	2,857	158	600-6,250	79
Sept.	256	3.1	235-269	330	7.5	297-374	2,770	533	750-6,500	11
Oct.	242	3.8	212-257	308	16.8	186-370	1,137	71	700-1,400	10
					Eastern Atlantic					
May	211	1.8	200-225	190	4.2	155-219	2,758	318	1,540-6,820	17
June	213	2.6	204-230	189	5.9	167-235	3,148	403	1,780-6,280	12
July	214	2.3	189-244	169	5.8	130-263	1,493	117	700-3,580	30
August	207	2.2	197-232	149	5.6	125-226	1,112	85	840-1,980	16

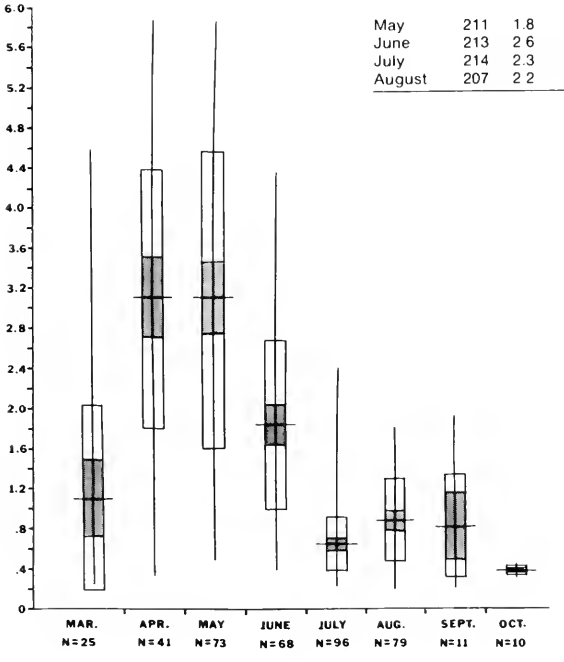


FIGURE 1.—Seasonal variation in gonosomatic index of 403 female giant western Atlantic bluefin tuna collected from 1965 through 1968 and 1974 through 1978. The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each side of the mean (shaded box) are shown.

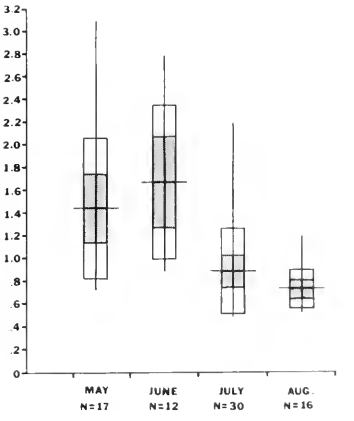


FIGURE 2.—Seasonal variation in gonosomatic index of 75 female giant eastern Atlantic bluefin tuna collected during 1963 by Rodríguez-Roda (1967). The number, mean (horizontal line), range (vertical line), 1 SD on each side of the mean (open box), and 2 SE on each of the mean (shaded box) are shown.

and reached a peak during April and May as indicated by the highest GSI. Sampling was inadequate for November through February. Well-developed ovaries were present mainly during May and June in eastern Atlantic giant bluefin tuna from the traps at Barbate (Rodríguez-Roda 1967). In May, the mean GSI for the western Atlantic was greater than that for the eastern Atlantic. No great difference was found between the mean GSI for the western and eastern Atlantic giant bluefin tuna for June, July, and August for which data were available for comparison. The plots of the GSI indicate that giant bluefin tuna spawning occurs earlier in the western Atlantic (the drop in GSI occurring in June) than in the eastern Atlantic (the drop in GSI occurring in July).

Heterogeneity of Egg Diameters

A significant difference in egg diameters was found for the center, midregion, and periphery of the anterior section of an ovary from a mature fish ($F=6.1$; df $=2, 631$; $P<0.005$). No significant difference in egg diameters was found for the center, midregion, and periphery of the middle or posterior sections of the ovary. A significant difference in egg diameters was also found among the anterior, middle, and posterior sections ($F = 11.6$; df $= 2, 1{,}843$; $P<0.001$). Because some heterogeneity occurred, estimates of fecundity were based on eggs from each section of both ovaries. Heterogeneity of egg size within an ovary has also been shown for albacore, *Thunnus alalunga*, (Otsu and Uchida 1959); swordfish, *Xiphias gladius*, (Uchiyama and Shomura 1974); and white marlin, *Tetrapturus albidus*, (Baglin 1979).

Histology of the Ovaries

Microscopic examinations were made of ovarian tissues from 119 small and medium bluefin tuna and 173 giant bluefin tuna. Diameters measured from these prepared slides were considerably smaller than those measured from whole eggs fixed in 10% Formalin (see footnote 5).

The oocytes were grouped into the following stages of oogenesis using the system of Kraft and Peters (1963), Smith (1965), and Moe (1969).

Stage 1—Thin layer of cytoplasm surrounding a relatively large nucleus with a single nucleolus; oocytes are <0.03 mm in diameter.

Stage 2—Dark cytoplasm and many peripheral nucleoli are in the nucleus oocytes are 0.03 mm through 0.13 mm in diameter (resting stage).

Stage 3—Yolk vesicles appear in cytoplasm; the membrane called the zona radiata, also referred to as zona pellucida (Hoar 1969) and vitelline membrane (Bodola 1966), appears at the end of this stage; oocytes are 0.17 mm through 0.30 mm in diameter (early vitellogenic stage).

Stage 4—Thick zona radiata, yolk vesicles, and yolk globules are present; oocytes are 0.33 mm through 0.63 mm in diameter (late vitellogenic stage).

Stage 5—This final stage was seldom observed during histological analysis. It evidently takes place during a short period of time immediately before ovulation. Eggs in this stage have a lightly staining granular yolk mass with few yolk vesicles and yolk globules, a thin zona radiata, and an irregular shape caused by sectioning.

Histological examination of female bluefin ovary sections from the Middle Atlantic Bight revealed the following:

Age 1—Very little sexual differentiation was present in age 1 bluefin tuna ($N = 17$) collected during May, June, July, and August. Some oogonia were observed within the lamellae.

Age 2—The first appearance of oocyte development occurred in age 2 bluefin tuna collected during July ($N = 4$). Both stage 1 and stage 2 oocytes were present, although stage 2 oocytes were most numerous.

Age 3—Many stage 2 oocytes and a few stage 1 oocytes were found in age 3 bluefin tuna collected during January and June ($N = 13$). Only stage 2 oocytes were found in age 3 bluefin tuna collected during July and August ($N = 10$).

Age 4—Stage 2 oocytes were present in all age 4 females collected during June ($N=36$) (Fig. 3). Also in 11% of these fish, some vitellogenic stage 3 oocytes undergoing absorption were present. Only stage 2 oocytes were present in age 4 bluefin tuna collected during July and August ($N = 10$).

Age 5—Mostly stage 2 oocytes were present in age 5 fish collected during June ($N = 16$),

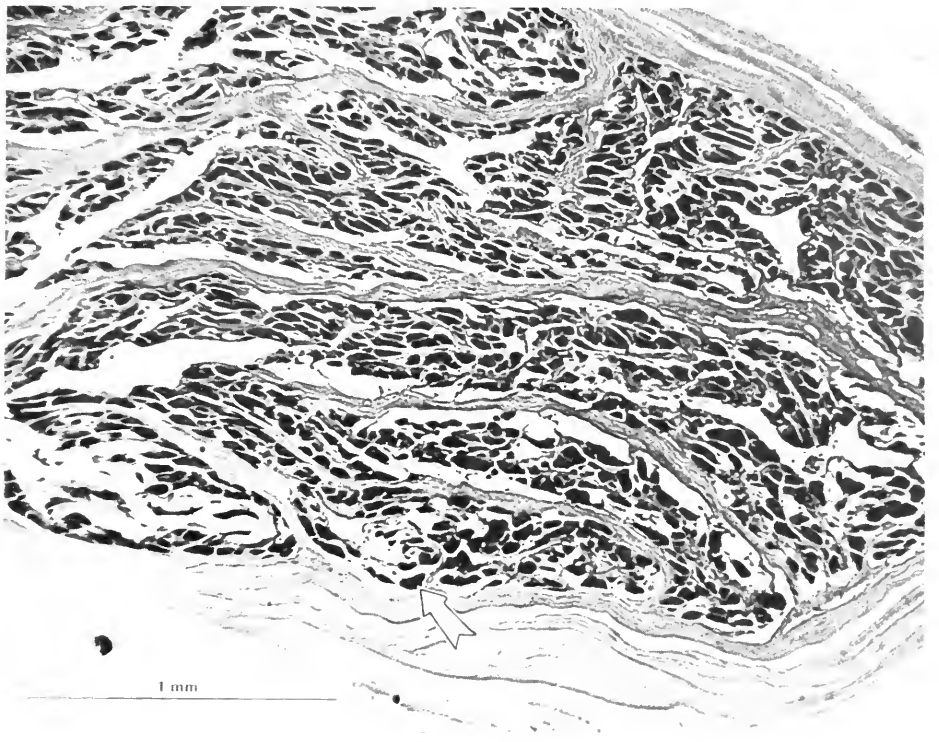


FIGURE 3.—Ovarian tissue from an age 4 bluefin tuna (119 cm, 33.6 kg) collected off the Middle Atlantic Bight during June 1977. Stage 2 oocytes are present, as indicated by arrow.

although a few stage 1 oocytes were also observed. Also, in 44% of these fish some stage 3 oocytes were present, many undergoing absorption. One individual also had some stage 4 oocytes present. These oocytes were in the process of degeneration. Mostly stage 2 oocytes were present in age 5 fish collected during July ($N = 2$). Both of these fish also had some stage 3 oocytes present, which were undergoing absorption. Stage 2 oocytes were present in all fish collected during August ($N = 4$). Only one of these fish had stage 3 oocytes present. These stage 3 oocytes were also undergoing absorption.

Age 6—The majority of oocytes observed in age 6 bluefin tuna collected during June ($N = 12$) were in stage 2 of development and only a few stage 1 oocytes were observed. Many of these fish (83%) had some stage 3 oocytes present, most undergoing the process of degeneration (Fig. 4). One individual had some stage 4 oocytes present, which were also degenerating. Only stage 2 oocytes were found in an age 6 bluefin tuna collected during August.

Age 7—Mostly stage 2 oocytes were found in age 7 fish collected during June ($N = 15$). Also, some stage 1 oocytes were present in most of these fish and 47% had stage 3 oocytes present, many of which were undergoing absorption. Only stage 2 oocytes were found in an age 7 fish collected during July and another age 7 fish taken during October.

Some gonadal development, therefore, occurs in these medium female bluefin tuna. However, the simulation of gonadal maturation by young fish that probably do not spawn has been reported for king mackerel, *Scomberomorus cavalle*, (Beaumariage 1973) and Atlantic sailfish, *Istiophorus platypterus*, (Jolley 1977). These authors based their determination on the size of the stage 4 oocytes, on their compactness within the lamellae, and on the appearance of many degenerating oocytes. My observations of medium bluefin tuna seem to correspond with the findings of the above authors, although the most

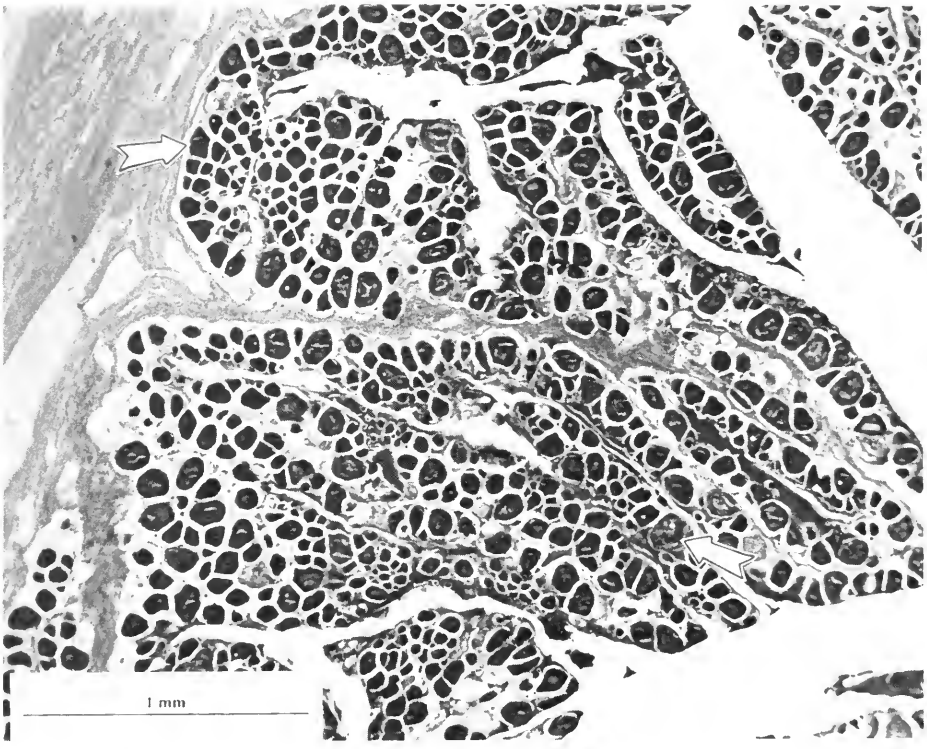


FIGURE 4.—Ovarian tissue from an age 6 bluefin tuna (153 cm, 59.5 kg) collected off the Middle Atlantic Bight during June 1976. Resting stage 2 oocytes are present (upper arrow), as are stage 3 oocytes undergoing the process of degeneration (lower arrow).

developed oocytes in the majority of fish that I examined were in stage 3 of development, and the average were in stage 2 based on the mean size of the oocytes measured (Fig. 5).

I believe, therefore, that the Middle Atlantic Bight is not a significant spawning area during the summer and probably not at any other time of the year, but samples are not available for other seasons. Also, recently there has been speculation by Rivas (1978) that some of these medium bluefin tuna may migrate during May and June across the Atlantic to the Mediterranean Sea to spawn. According to Sella (1929) eastern Atlantic bluefin tuna begin to reproduce in their third year, when they attain a weight of about 15 kg. Rodríguez-Roda (1967) found that 50% of eastern Atlantic bluefin tuna females are mature at 97.5 cm or 3 yr of age. However, the smallest bluefin tuna that he estimated fecundity for was 130.5 cm and 54 kg, which corresponds to an age 5 fish according to Coan (1976). Frade and Manaças (1933) found very little development in age 3 females from the eastern Atlantic. Cort et al. (1976) found developing oocytes in eastern Atlantic bluefin tuna measuring 148 and 152 cm from the Gulf of Gascony. These fish would be age 6 according to Coan (1976).

The only published record I have found of age of maturity of western Atlantic bluefin tuna is that of Westman and Neville (1942). Observing the gross morphology of ovaries, they indicated that western Atlantic bluefin tuna 5 yr of age appeared to be mature, although the gonads gave no indication of the presence of eggs. I have also examined the unpublished cruise report of the MV *Delaware*, June 1957. Using the conversion table of Coan (1976), all age 3 female bluefin tuna were judged immature, and most age 4 (2 out of 3) were judged immature. No description of the ovaries on an age 5 fish was given, and 67% of age 6 females ($N = 6$) had well-developed eggs.

My analysis of western Atlantic bluefin tuna ovaries indicates that age 6 would probably be

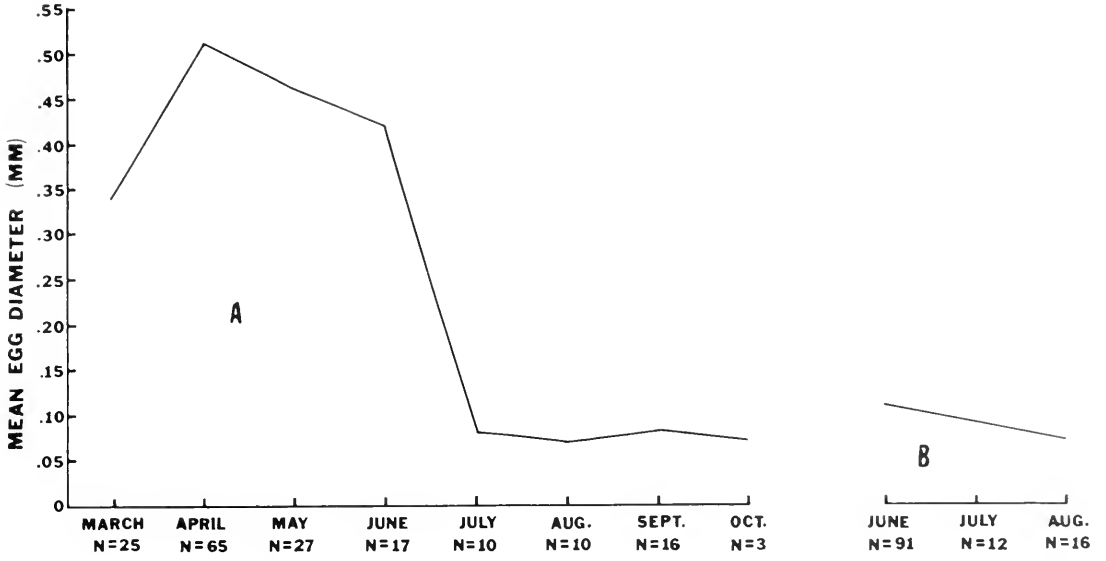


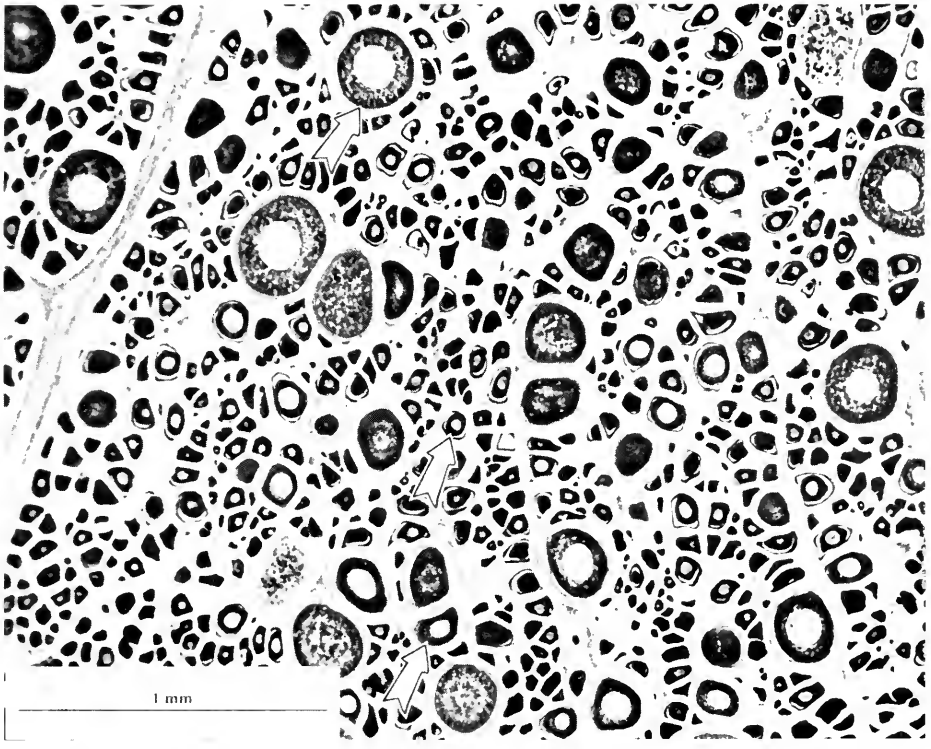
FIGURE 5.—Mean egg diameter of largest ovarian egg as determined from histological sections from monthly samples (N) of A) female giant bluefin tuna from the Gulf of Mexico and the Florida Straits (March through June 1955, 65-67, 76-78) and from off New England (July through October 1974-75, 77), and B) female bluefin tuna ages 3-7 from off the Middle Atlantic Bight (June through August 1974-77).

the earliest age at which a majority of females could possibly reach maturity. However, a majority of vitellogenic oocytes in these age 6 fish were being absorbed and most likely would not have been spawned during the years when these fish were taken. As previously noted, I observed no vitellogenic oocytes in age 3 fish, but if Sella (1929) and Rodríguez-Roda (1967) are correct, eastern Atlantic bluefin tuna may reach maturity at an earlier age than their western Atlantic counterparts.

Vitellogenic oocytes were not found in the two giant bluefin tuna (205 and 207 cm) taken during the March 1966 MV *Delaware* Cruise 66-2 (lat. 37°24'N, long. 67°32'W). Vitellogenic oocytes were found in one of three giant fish (190-213 cm) taken during April 1965 on the MV *Delaware* Cruise 65-3 (lat. 35°54'N, long. 72°51'W). Evidently this area of the western North Atlantic was not an important spawning area for bluefin tuna during March-April.

Vitellogenic oocytes (stages 3 or 4) were present in all giant bluefin tuna taken from the Gulf of Mexico and Florida Straits during 1955, 1967, 1976, 1977, and 1978 during March (N = 24), April (N = 61), and May (N = 54) (Figs. 6, 7). In one of two fish taken in June 1967 and 1977, stage 3 and stage 4 oocytes were present; in the other fish all the vitellogenic oocytes had been spawned or absorbed. On the average, the largest oocytes in all of the fish for July (N = 10), August (N = 10), September (N = 16), and October (N = 12) from off New England during 1974, 1975, and 1977 were in stage 2 (Fig. 8). Vitellogenic oocytes were generally absent from these fish.

I found degeneration and absorption of advanced unovulated eggs more common as the season progressed. This agrees with the findings of Frade and Manaças (1933) for eastern Atlantic bluefin tuna. Distinctive atretic bodies, formed from the remnants of oocytes that were not shed, were present in the female giant bluefin tuna collected during March through October. Topp and Hoff (1971) also reported atretic body formation in the ovaries of a single giant female collected from the west Florida coast during May. As previously described by Smith (1965), these atretic bodies form a characteristic brownish mass, the corpus atreticum, and are made up of amorphous brownish granules, phagocytes, and clear yellow pigment globules (Fig. 9). I found that empty follicles left behind after the ripe oocytes are released degenerate rapidly. This was also observed for eastern Atlantic bluefin tuna by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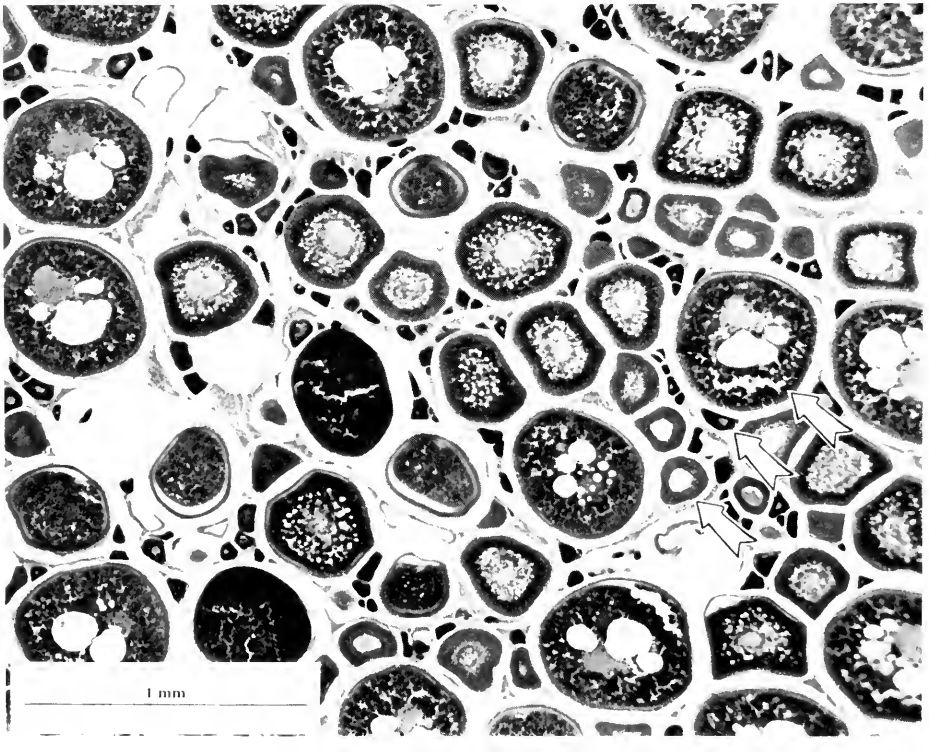
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FIGURE 6.—Ovarian tissue from a giant bluefin tuna (250 cm) collected off the Gulf of Mexico during March 1978. Early stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

FIGURE 7.—Ovarian tissue from a giant bluefin tuna (205 cm) collected off the Gulf of Mexico during May 1978. Late stage 4 oocytes (upper arrow), stage 2 oocytes (middle arrow), and stage 3 oocytes (lower arrow) are present.

Frade and Manaças (1933), who speculated that the rapid degeneration of the follicles could be caused by pressure exerted by neighboring oocytes. My findings also confirm that western Atlantic bluefin tuna released eggs intermittently during April, May, and June, the majority during May.

Fecundity Estimates

Fecundity estimates were obtained for 28 western Atlantic bluefin tuna, which were collected from the Gulf of Mexico and Florida Straits during April, May, and June of 1967, 1968, 1974, 1975, 1976, and 1978 (Table 4). The reliability of the dry gravimetric method was tested by estimating the fecundity of an individual fish by counting and weighing eggs from four subsamples. Based on these four estimates, the average number of eggs >0.46 mm in diameter was 41.6 million with a range from 40.0 to 43.0 million and a standard error of the mean (SE) of 0.76. The average number of eggs >0.32 mm in diameter was 76.0 million with a range from 72.5 to 82.5 million and SE = 2.2.

I am presenting two estimates of potential fecundity, and the estimate based on eggs >0.32 mm in diameter essentially coincides with the size of 0.33 mm used by Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. This would be the potential number of eggs that could be spawned, assuming there was no degeneration or absorption of advanced unovulated eggs. My histological examinations of bluefin ovaries,

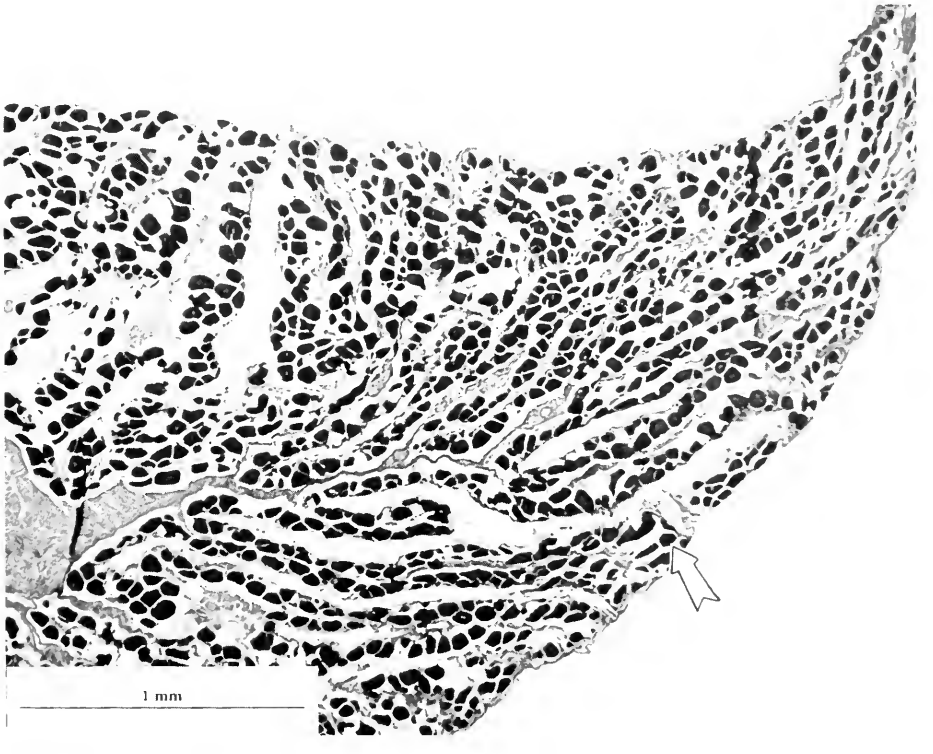

FIGURE 8.—Ovarian tissue from a giant bluefin tuna (256 cm, 268 kg) collected off the northeast coast of the United States during August 1975. Stage 2 oocytes are present, as indicated by arrow.

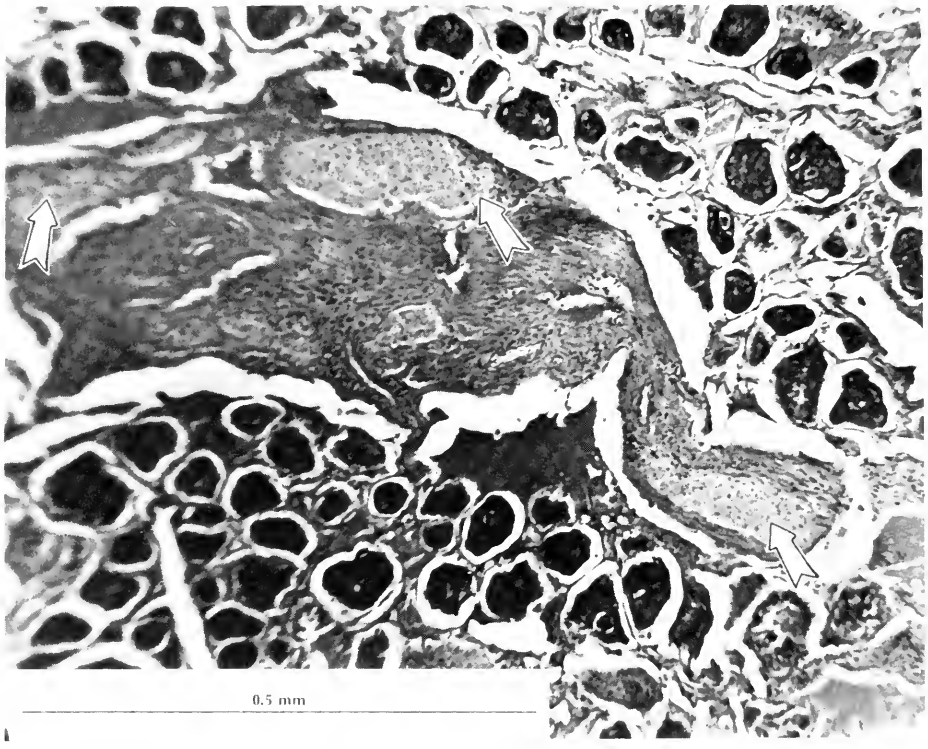

FIGURE 9.—Ovarian tissue from a giant bluefin tuna (264 cm, 297 kg) collected off the northeast coast of the United States during July 1975. Brown bodies are present, as indicated by arrows.

however, revealed the presence of atretic bodies. It was impossible to quantify the number of eggs constituting these atretic bodies, although I assume that absorption would occur principally with the smaller vitellogenic ova. Therefore, I have also estimated the number of eggs >0.46 mm in the most advanced size mode that could potentially be spawned during one spawning season. For bluefin tuna 205-269 cm FL and 156-324 kg round weight, the average number of eggs 0.33 mm in diameter and larger was estimated as 60.3 million (SE = 4.04) and the average number of eggs 0.47 mm in diameter and larger was estimated as 34.2 million (SE = 2.15). No apparent relationship was found for fecundity as a function of length or estimated weight for the size range of bluefin tuna I studied. MacGregor (1968) said that the relationships of length and weight to egg production are masked in many species of fish, because egg production occurs over a relatively short range in size, and because variation in number of eggs produced at each length is great. Bailey (1964) found no obvious relationship between fecundity and fish size for American smelt, *Osmerus mordax*. Schenck and Whiteside (1977) and Loesch and Lund (1977) found a great amount of variability in fecundity for a given fish size for the fountain darter, *Etheostoma fonticola*, and blueback herring, *Alosa aestivalis*. Since histological examinations of ovaries and estimated GSI showed that the bluefin tuna are multiple spawners, it is possible that some of the fish selected for fecundity estimates had previously shed eggs. Also the rate of absorption of vitellogenic ova could have varied for the fish selected for fecundity estimates. I found, however, that the dry weight of eggs could be used for estimating fecundity. The following relationships were found:

$$F = 5.2895 + 0.0167\ W\ (R^2 = 0.64),$$

where F is the number of ova >0.46 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

TABLE 4.—Length, weight, and gonadal data for 28 female western Atlantic bluefin tuna from the Gulf of Mexico and the Florida Straits collected during April, May, and June 1967, 1968, 1974, 1975, 1976, and 1978. The mean and standard error of the mean are given at the bottom of the columns.

Body length (cm)	Estimated body weight (kg)	Dry weight of eggs (g)	Gonosomatic index (%)	Estimated no. of eggs: 0.46 mm diameter (millions)	Estimated no. of eggs: >0.32 mm diameter (millions)
205	156	1,260	5.3	13.6	32.7
222	[1]188	696	2.1	16.7	22.7
229	217	1,202	3.1	24.2	46.4
229	217	2,177	5.0	55.5	96.0
229	217	1,481	2.8	33.9	64.4
231	224	1,330	4.4	26.8	41.1
236	[1]197	1,329	3.2	28.4	40.3
236	[1]189	1,404	3.2	29.6	44.7
238	246	1,788	4.1	39.0	63.9
238	246	1,703	4.2	40.1	64.5
238	246	1,796	3.8	34.4	61.7
241	254	1,483	3.4	29.8	62.4
241	254	2,436	4.8	48.0	84.9
241	[1]247	1,560	3.9	33.0	44.0
244	263	1,750	3.6	25.2	56.7
244	263	1,452	3.4	23.2	42.1
244	263	2,121	5.0	49.3	93.3
252	289	2,770	4.7	39.6	94.6
254	298	1,942	2.9	41.6	76.0
—	307	1,681	2.5	32.0	59.2
256	307	1,950	2.6	42.2	79.5
257	[1]232	1,200	2.9	24.3	33.8
257	309	750	1.9	16.2	26.2
259	316	2,750	4.2	32.6	76.9
259	316	2,500	4.4	48.8	80.6
261	[1]272	1,488	2.6	31.4	42.3
262	[1]324	2,593	4.5	57.6	81.6
269	[1]284	1,950	4.6	40.6	74.8
$\bar{X}$ 243	255	1,734	3.7	34.2	60.3
SE 2.78	8.37	102.79	0.18	2.15	4.04

[1]Actual weight determined.

$$F = -0.9057 + 0.0353\ W\ (R^2 = 0.81),$$

where F is the number of ova >0.32 mm in diameter and W is the dry weight of all eggs separated from the ovarian connective tissue.

A reduction in fecundity in older fish has been reported by Bodola (1966) for gizzard shad, *Dorosoma cepedianum*, and by Loesch and Lund (1977) for blueback herring. No such decline in number of eggs was found for western Atlantic bluefin tuna.

My fecundity estimates for western Atlantic bluefin tuna are considerably greater than the estimate given by Williamson (1962). He, however, did not describe how he arrived at his estimate for a western Atlantic bluefin tuna. My estimates more closely agree with estimates presented by Frade (1950) and Rodríguez-Roda (1967) for eastern Atlantic bluefin tuna. Although my estimates were based generally on larger fish, it appears that western Atlantic bluefin tuna are considerably more fecund than eastern Atlantic bluefin tuna.

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AN EVALUATION OF TECHNIQUES FOR TAGGING SMALL ODONTOCETE CETACEANS

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ABSTRACT

Ninety tags—various combinations of radio tags, spaghetti tags, Roto tags, freeze brands, and tags bolted to the dorsal fin—were placed on 47 Atlantic bottlenose dolphins, *Tursiops truncatus*, captured near Sarasota, Florida, between January 1975 and July 1976. In 18 months of field observation, 910 tagged dolphins were sighted; 781 were identifiable, and 129 were not. Twelve naturally marked dolphins were also observed. Radio tagged animals were tracked for as long as 22 days. Repeated observations of tagged animals permitted evaluation of effect on animals and relative merits of the various tags. Freeze brands were most readable from a distance (≤30 m), and most long lived (4.8 years). Other tags were too short lived (bolt tags) or too small to be identified from a distance (Roto tags and spaghetti tags), and all caused tissue destruction. Radio tags caused unexpected dorsal fin damage and were frequently lost prematurely. Taken together, the results suggest that freeze brands are least harmful, and that static tags should be tested on each species to be studied prior to attachment in the field.

Cetaceans are difficult to study in the field. Most individuals move almost constantly, rise to the surface only briefly to breathe, and are difficult to differentiate from conspecifics. To facilitate individual recognition, researchers have developed several tagging techniques and tested them on small odontocete cetaceans. Nishiwaki et al. (1966) placed streamer tags on captive roughtoothed dolphins, *Steno bredanensis*, and concluded that none were effective. On the other hand Perrin et al. (1979) recovered spaghetti tags, another type of streamer, from free-ranging dolphins, *Stenella* spp., in the eastern tropical Pacific up to 1,478 d after attachment. Roto tags were placed on the spotted dolphin, *S. attenuata*, and one marked individual was repeatedly identified from a semisubmersible over a period of 3½ yr (Norris and Pryor 1970). Evans et al. (1972) successfully used radio transmitters, large plastic "button" tags, spaghetti tags, and freeze brands on a total of five species in the Pacific Ocean and Gulf of Mexico. Leatherwood and Evans (1979) have recently reviewed developments and uses of radio tags on cetaceans. Irvine and Wells (1972) reported that an improved button tag was sighted 3 mo after attachment to a bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Fla. Despite all these improvements in tagging technology, however, little information has been available about long-term effectiveness or affect on the wearers of any type of tag.

The tagging program of Irvine and Wells (1972) was reinitiated in the same area in January 1975, after a 4-yr lapse. Using radio transmitters, visual tags, and natural marks we studied the movements and activities of bottlenose dolphins. Between 29 January 1975 and 25 July 1976, 47 dolphins were captured, tagged, and released a total of 90 times. A summary of the tagging program and an evaluation of the tagging methods used are included below. Detailed analysis of the tagging program results is presented by Irvine et al. (1979,[4] 1981).

METHODS

The study was conducted along 40 km of coast south from Tampa Bay, Fla. The study area included shallow channels and bays bounded by a chain of barrier islands (NOS Chart No.

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[4]Irvine, A. B., M.D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, including an evaluation of tagging techniques. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-298042, 54 p.

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11425). Dolphins were captured by encircling one to nine animals with a 455 m × 4.5 m net dropped from a fast moving boat in shallow water. An inner circle enclosure method (Asper 1975) was used to minimize escapes. The inner circle was partitioned so that individual dolphins could be isolated and entangled without collapsing the entire net on remaining animals. Tangled dolphins were removed from the net and placed for tagging in a stretcher, usually held in the water alongside a boat. All animals were sexed, measured, and photographed before tagging. Previously tagged dolphins were examined and retagged as necessary before being released.

The study area was surveyed as thoroughly as possible at least biweekly in a 7.3 m Wellcraft Fisherman[5] boat equipped with a 3 m tuna tower. All dolphin sightings were recorded during 228 surveys; photographs were taken to facilitate identification of tags and distinctive dorsal fins.

Radio Tags

An improvement (Model PT 219) of the radio tag developed for small pelagic cetaceans by Ocean Applied Research Corporation (Martin et al. 1971) had not been tested on *T. truncatus*. In our first efforts, the transmitter was attached with plastic straps to a foam-lined fiber glass saddle and secured to the dorsal fin with a stainless steel bolt through the fin. Because saddles provided by the manufacturer were too small for most *T. truncatus*, the transmitters were attached to fiber glass saddles molded by the authors (Fig. 1A, C). The saddles were lined with open cell foam to protect the animal from abrasion and to allow water circulation for thermoregulation.

Transmitter saddles were attached using techniques developed by other investigators (see review by Leatherwood and Evans 1979). The first seven saddles were attached with single bolts through the dorsal fin. The last three saddles were attached with bolts fore and aft to provide greater stability against water flow (Fig. 1C). Spring-loaded bolts with dissolving nuts were designed to release the saddle and transmitter from the dolphin sometime after the 1-2 mo life of the lithium batteries.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA, or the U.S. Fish and Wildlife Service.

Ten radio tags (designated RT-1 through RT-10) were attached to dolphins between 29 January 1975 and 9 June 1976. The RT-1 transmitter consisted of a single 35 cm long × 3.7 cm diameter tube with a 63 cm high spring steel antenna on the forward end. Transmissions from RT-1 gradually failed within 2 h, apparently due to saltwater leakage into the battery case. Cause of failure could not be confirmed because the transmitter was missing from the saddle when it was sighted 2 d after attachment. Transmitters on subsequent radio tags were attached to the saddle with bolted aluminum plates (Fig. 1A, C) instead of plastic straps.

The transmitter antenna on RT-2 was observed to be broken off at the base 5 d after attachment. Consequently, transmitter packages on RT-3 through RT-10 were modified to two tubes, 19.2 cm long × 3.8 cm diameter, connected by copper tubing at the forward end. A flexible 42.5 cm high whip antenna extended vertically from the rear of the starboard tube. The tubes, with transmitter assembly in one and batteries in the other, were bolted to either side of the saddle, and the connecting tubing was solidly encased in fiber glass (Fig. 1C).

Visual Tags

The button tags described by Evans et al. (1972) had proven not to be durable on *T. truncatus* (Irvine and Wells 1972). Therefore, we elected to try rectangular fiber glass "visual tags" (Fig. 2). These tags were 10 cm × 7.5 cm and made of 0.4 cm thick yellow laminated fiber glass with 5.1 cm high black tape numerals epoxied to the surface. Each tag was held in place by Teflon bolts with stainless steel washers and cotter pins. The bolts were placed near the anterior edge of the tag to produce a streaming effect as the dolphin moved through the water. The bolt hole was bored through the fin and cauterized with a heated rod, and sheathed with Plexiglas tubing in the same manner as for radio tags.

Double bolt tags, also yellow rectangles with black numerals, were cut from 0.2 cm thick fiber glass and varied in size from 9.0 cm × 12.9 cm to 10 cm × 15 cm, depending on the size of the dorsal fin to be tagged. The bolts were located near the anterior and posterior edges of the tag. Numerals were 7.7 cm high. Because cotter pins had sheared some of the Teflon bolts on single

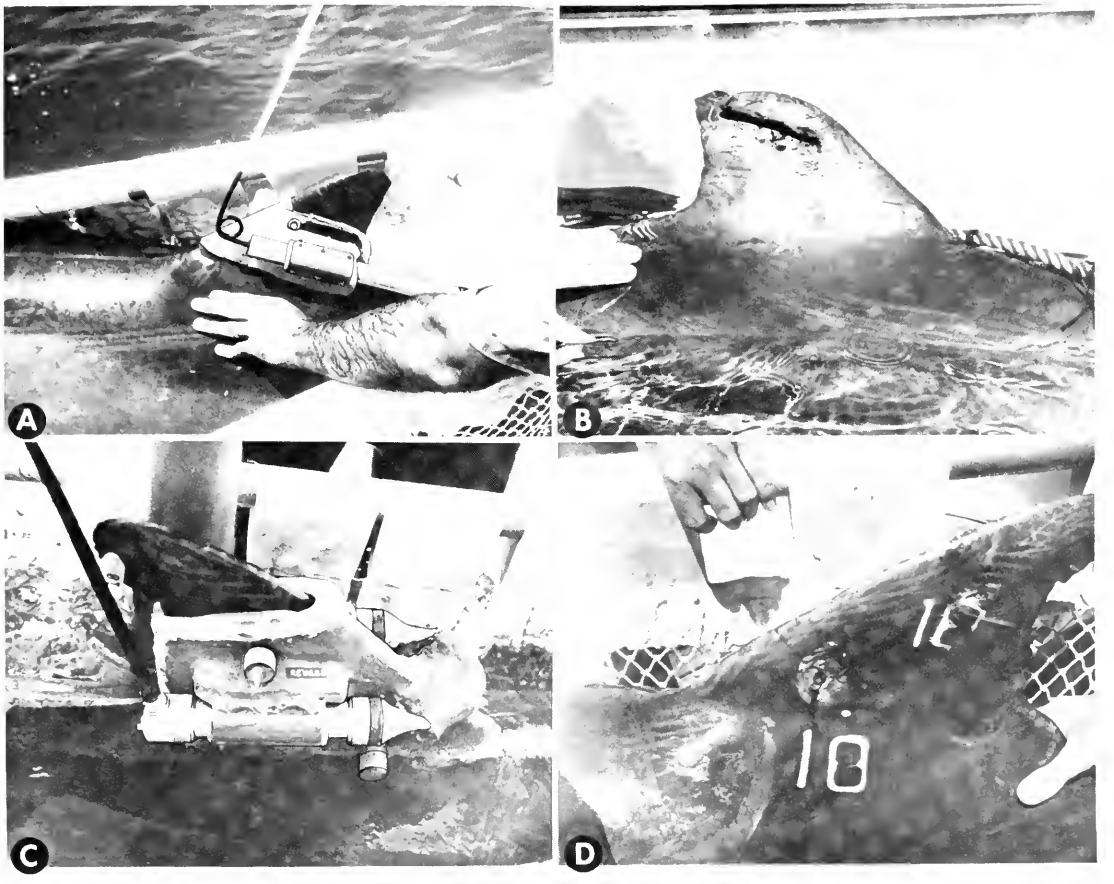

FIGURE 1.—A. Single tube transmitter with spring antenna forward (on dolphin RT-2). B. Dorsal fin 8 mo after transmitter in A was attached. C. Twin tube transmitter assembly with whip antenna aft. Dissolving nuts are top center and below the forward portion of the tube. D. Dorsal fin from C 22 d after the transmitter's installation. Note discolored, apparently necrotic, area around forward hole and apparent migration path of top bolt.

bolt tags, double bolt tags were attached with 0.64 cm stainless steel bolts and nuts.

Freeze Brands

When first captured, all dolphins were freeze branded with 5 cm high numerals on both sides of the dorsal fin and on the body below the fin (Figs. 1D, 2C, D). Recaptured animals were rebranded as necessary to improve visibility of existing brands. Application times of 15 s with irons cooled in a mixture of Dry Ice and alcohol were used to brand the dolphins captured before August 1975. Thereafter, liquid nitrogen was used as the coolant. The application time remained 15 s. When possible, the skin was rubbed with an alcohol swab to lower the skin temperature by evaporative cooling prior to branding. Before April 1976, the branding irons were applied to the skin with a gentle rocking motion to assure even contact. After that time the irons were held firmly against the skin without motion, and brand visibility was greatly improved. In some cases, however, parts of the brand did not show because of uneven contact (Figs. 1D, 2C, D).

Roto Tags

Numbered Roto tags (NASCO Inc., Ft. Atkinson, Wis., Jumbo size) were attached to the trailing edge of the dorsal fin of all dolphins handled after January 1976. Red tags were attached to females and yellow tags to males. The

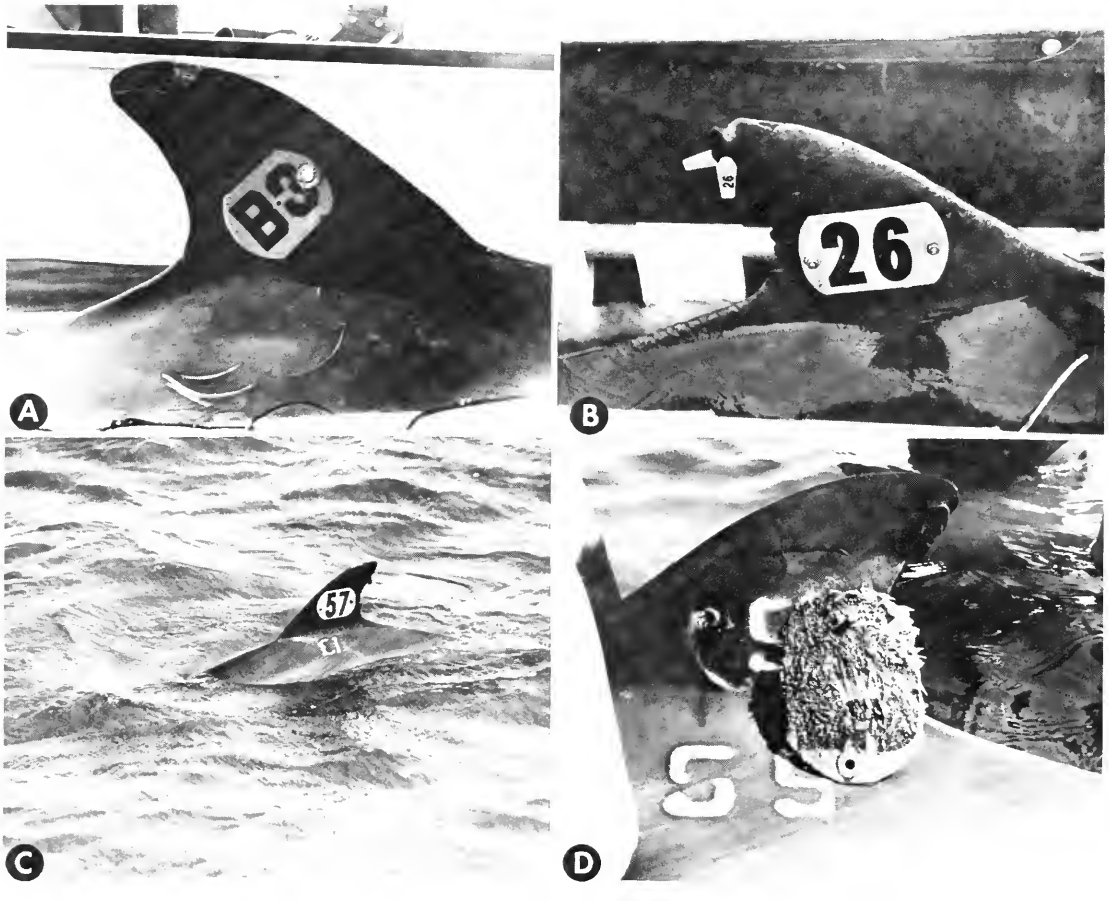

FIGURE 2.—A. Single bolt visual tag held by Teflon bolt and cotter pin. Note tag bolt scar from 1970-71 study. B. Double bolt tag, Roto tag (at top rear of fin), and spaghetti tag (lower right). C. Double bolt tag on free-swimming dolphin. Note freeze brand with incomplete left digit on body below fin. D. Algae-covered tag 2 mo after initial installation. Note indented area of skin where water flow against tag on opposite side of fin caused pressure on near side. Note also discolored tissue around forward bolt hole.

TABLE 1.—Comparison of tagging techniques.

Tag no.	No. tags installed	Tag longevity[1]	No. sightings/tag mean	No. sightings/tag total	No. identifications/tag mean	No. identifications/tag total	% identifiable sightings-other observers	No. tags of known fate	Tags of known fate lost, broken, or removed %	Tags of known fate lost, broken, or removed total no.	Tags of known fate obscured by fouling %	Tags of known fate obscured by fouling total no.	Tags of known fate removed because of tissue damage %	Tags of known fate removed because of tissue damage total no.
Visual tags (single bolt)	16	<5 min to >2 mo	4.88	78	2.00	32	6	14	86	12	14	2	14	2
Visual tags (double bolt)	19	<2 wk to >2 mo	10.00	190	9.84	187	16	16	63	10	31	5	25	4
Roto tags	53	<1 d to >5.5 mo	6.45	342	0.53	28	0	48	40	19	10	5	4	2
Spaghetti tags	17	<1 mo to >13 mo	2.53	43	0		0	12	50	6	0		25	3
Freeze brands	[2]47	>4.8 yr	6.57	309	5.89	277	2	39	—	—	—	—	—	—
Natural marks[3]	12	>6 yr	7.25	87	7.25	87	1	12	—	—	—	—	—	—

[1]Length of time tag was attached and identifiable.
[2]Many were redone or "touched up."
[3]Recognizable dorsal fins.

numbers on the tags were too small to be read from the observation boat, but the color codes were useful for recognition of sex, and the positions of a tag often indicated identity.

Spaghetti Tags

Spaghetti tags (Floy Tag and Manufacturing, Inc., Seattle, Wash., Model FH 69A) were tested on some dolphins captured from April through June 1976. The attachment technique was similar to that described by Evans et al. (1972), except that the tags were applied to animals in a stretcher.

Natural Marks

Some dolphins had disfigured or uniquely shaped dorsal fins. A photo catalog of these recognizable untagged animals was compiled as a reference for field identification.

RESULTS

Nine hundred ten tagged dolphins were sighted; 781 were identifiable, and 129 others were not. When field identification was uncertain, photographs of combinations and locations of tags or tag remnants were often examined to verify individual identities. A compilation of tagging and sighting results is presented in Table 1.

Radio Tags

Ten dolphins were radio tagged and tracked for up to 22 d (Table 2). Eight of these were later recaptured and examined. In five instances, the saddle was lost, apparently because the bolt ripped through the fin (for example, see Figure 1B). Fin damage was apparent 3 to 6 wk after tagging by which time saddles no longer fit snugly over the leading edge of the fin. When loosened, the saddles tilted backwards creating an obvious drag; this shifting caused the bolts to migrate dorsoposteriorly. When RT-8 was recaptured after wearing a transmitter for 22 d, the two bolt holes had not healed nor appeared infected. The forward bolt had migrated dorsoposteriorly about 1.5 cm (Fig. 1D), and the saddle was fouled with algal growth and monofilament line. When RT-9 was recaptured after 46 d, the saddle and rear bolt were missing, but the front bolt was still present but bent, with part of the dissolving nut attached. The partially healed wounds appeared discolored and necrotic, but showed no obvious signs of infection. Only RT-6 showed no fin damage from the radio tag, but the tag (with malfunctioning transmitter) was removed <8 h after attachment.

Two dolphins, RT-9 and RT-10, developed aberrant swimming behavior after 10 and 17 d, respectively. Both animals were observed to respire without bringing the dorsal fin to the surface in a typical cetacean rolling motion, although each could move rapidly under water. Evaluation of the problem was impossible because RT-9 evaded recapture attempts during this period, and RT-10 was not sighted during capture operations.

One animal, RT-7, died 17 d after tagging, apparently of causes unrelated to the radio tag. Necropsy results implicated pulmonary damage from parasitism as a cause of death. It could not be determined if the capture-tagging process contributed to the cause of death. Tissue autolysis precluded histopathological examination, and no parasites were found.

TABLE 2.—Radio tagging results.

Tag no.	Tag description	Dolphin sex	Dolphin length (cm)	Date attached	Duration of transmission	Probable reason for cessation of transmission
RT-1	Single cylinder; forward spring antenna	Male	251	29 Jan. 1975	2 h	Water leak (?)
RT-2	Single cylinder; forward spring antenna	Male	210	28 Apr 1975	5 d	Broken antenna
RT-3	Twin cylinder, aft spring antenna	Male	249	15 Jun. 1975	20 h[1]	Seawater switch failure (?)
RT-4	Twin cylinder; aft flexible antenna	Female	252	1 Aug. 1975	6 d[2]	Unknown
RT-5	Twin cylinder; aft flexible antenna	Female	257	2 Oct 1975	7 d[3]	Seawater switch failure (?)
RT-6	Twin cylinder; aft flexible antenna	Male	226	15 Dec. 1975	7 h	Seawater switch malfunction; transmitter removed
RT-7	Twin cylinder; aft flexible antenna	Male	239	14 Feb. 1976	17 d	Functioning transmitter removed from dead dolphin after 21 d
RT-8	Twin cylinder; aft flexible antenna	Male	221	15 Apr. 1976	22 d	Functioning transmitter removed because of fin damage
RT-9	Twin cylinder; aft flexible antenna	Female	256	8 May 1976	10 d	Unknown. Dolphin did not bring fin above the surface
RT-10	Twin cylinder; aft flexible antenna	Female	250	9 June 1976	17 d	Unknown. Dolphin did not bring fin above the surface

[1]Inconsistent signals during the last 6 h.
[2]Direction finder malfunction after 6 d.
[3]Inconsistent signals during the last 3 d

Visual Tags

Sixteen single bolt tags were attached between January and December 1975. One was lost within seconds, and three others were lost within 24 h. Two tags had twisted after 2 mo, damaging the fin and requiring removal of the tag. Another tag was believed to have ripped through the fin of a third animal. Two recaptured dolphins had bolt migration scars, and the tags were lost. Of 32 single bolt tags identified in the field, only 3 were sighted more than 2 wk after tagging.

From December 1975 through May 1976, 19 dolphins were tagged with double bolt tags. Tags were identified on free-ranging dolphins 187 times through July of 1976, and one tag was sighted 2 mo after attachment. Broken tags were observed eight times, and nine sightings were unidentified due to algae and barnacle fouling (Fig. 2D). Several tags were observed to have only the upper anterior edges broken, implying that breakage was from physical contact. During recaptures, four intact tags were removed because barnacles on the inner surface of the tag caused skin abrasions. Six broken tags were removed. Bolt migration was not as common as with single bolt tags, probably because of the stability offered by the rear bolt. Although none of the bolt wounds appeared fully healed, none appeared infected when the animals were recaptured and examined.

Visual tags were often discernible up to 200 m away. The numerals were rarely readable at distances >50 m, but even broken tags, tag bolts, and tag scars were useful for identification of some dolphins.

Freeze Brands

Freeze brands were recognizable on marked animals at distances of <30 m, although photographic analysis was often necessary to confirm identification. Some brands were difficult to identify because they were incomplete or because of the relatively poor color contrast of the brand against the skin (Figs. 1D, 2C).

One of the dolphins captured by Irvine and Wells (1972) in March 1971 and freeze branded (on both sides of the dorsal fin) was captured again in December 1975. The animal had a readable freeze brand on only one side of the fin. On another dolphin branded in the same manner in March 1971 and additionally recognizable because of a deformed lower jaw, the brand was readable in May 1971 (Evans et al. 1972), but the brand was no longer visible upon recapture in February 1976.

Roto Tags

From February 1976 through July 1976, 53 Roto tags were placed on 38 dolphins, including 3 animals released with 2 tags. Roto tags were known to be lost from 17 animals and were replaced on 10 of them. A healed indented notch on the trailing edge of the fin was the only evidence of tag loss. Two Roto tags were replaced due to barnacle fouling on the inner surfaces. Brown algae and/or barnacles obscured the tag numbers on most recaptured dolphins, but the tags were still readable on close examination.

Roto tag color could be observed from up to 70 m in calm seas. When examined photographically, position of the tag on the fin or placement in relation to other tags or marks helped verify identity. No dolphins were identified exclusively with Roto tags.

Spaghetti Tags

Seventeen spaghetti tags were attached to 13 dolphins, including 4 dolphins initially released with two tags. None of the animals reacted noticeably to the attachment process. Six tags were missing from four animals recaptured 10 wk after tagging. Three tags were removed from three other dolphins because the entry wounds appeared to be festering.

Animals that had lost their tags bore healed but discolored scars that were similar in size to the festering entry wounds described above. No scratches or other evidence that the dolphins may have attempted to remove the tags by rubbing were noted. The wounds, up to 1.9 cm in diameter, apparently were created by movement of the base of the tag streamer on the skin.

One spaghetti tag was observed in May 1977, 345 d after attachment. Several orange colored spaghetti tags became faded within 4 wk, an observation not reported by other investigators.

Natural Marks

Twelve untagged dolphins with recognizable natural marks were identified a total of 87 times. Photographs of an individual taken first in 1970-71, then during this study in 1976, and by Wells

et al.[6] in 1980 suggest that natural marks are relatively permanent.

DISCUSSION

The most obvious shortcoming of tags attached to the dorsal fin was the short longevity. Water drag, tissue rejection, and attempts by dolphins to shed tags may have contributed to tag loss and fin damage. We had hoped that tissue would grow tightly around the bolt sheaths and insulate the wound from bolt-induced tissue irritation; however, healing apparently never occurred while bolts were in place. Since tag wounds did not heal, different attachment methods or new designs are needed. Transmitter packages on two killer whales, *Orcinus orca*, were held for 6 mo by pins implanted diagonally to the plane of the leading edge of the fin (Erickson[7]), and may offer an alternative method of attachment. The relatively larger fin of a killer whale (vs. a dolphin) may, however, have increased chances of success. Carbon bolts attach human prosthetic devices,[8] and are another attachment method yet to be tested on marine mammals.

Radio tags have proved useful to study the ecology of small odontocetes (Evans 1971, 1974; Evans et al. 1972; Gaskin et al. 1975; Würsig 1976), but the configuration used in this study is not recommended for use on *T. truncatus*. The fin damage, premature transmitter loss, and unusual swimming behavior which we observed, may influence study results. These factors have not been previously documented. Radio tags caused no obvious behavioral effects during captive tests on *Delphinus delphis* (Martin et al. 1971). In field studies, however, the radio tagged animals have been infrequently sighted and never recaptured, so possible long-term effects of the tags on the animals are unknown.

Freeze branding proved the most durable marking method. The variability of marks on the animals captured 5 yr after branding indicates that tissue response to the branding process is inconsistent. Freeze brands have remained readable after several years in captivity, but optimal coolants, application times, and pressures have yet to be determined (Cornell et al.[9]). Our resighting, after almost 5 yr, is the longest yet reported. Twenty-one of 26 of the dolphins originally tagged in this study were observed during 1980 and had freeze brands that were either completely readable in photographs or were legible enough to confirm identifications indicated by other characteristics (Wells et al. footnote 6). Maximum longevity of freeze brands is still unknown, however.

The comparatively high incidence of spaghetti tag loss reported here is noteworthy because this tagging method has been previously used with no reports of rejection or abscess (Sergeant and Brodie 1969; Evans et al. 1972; Perrin et al. 1979). Recent tests on captive dolphins have shown, however, that tag loss may be related to tissue rejection, attachment impact, or to the angle of dart entry (Jennings[10]).

Recognition of natural marks provided useful supplementary information in our study, and has been used to study bottlenose dolphins in Texas (Gruber 1981; Shane and Schmidly[11]) and Argentina (Würsig and Würsig 1977). Close approach to the animals is usually required for field recognition, however, and we felt that photoidentification was necessary to verify most of our sightings.

This tagging study has demonstrated that repeated sightings of tagged dolphins are possible and can provide substantial amounts of information about the behavioral ecology of small cetaceans (Wells et al. 1980; Irvine et al. 1981). Selection of the tags to be used should, however, involve consideration of tagging and resighting effort, tag visibility and durability, and potential harm to the tagged animal. Visual

[6]Wells, R. S., M.D. Scott, A. B. Irvine, and P. T. Page. 1981. Observations during 1980 of bottlenose dolphins, *Tursiops truncatus*, marked during 1970-1976, on the west coast of Florida. Report to National Marine Fisheries Service, Contract No. NA80-GA-A-195, 21 p. Available Center for Coastal Marine Studies, University of California, Santa Cruz, CA 95064.

[7]Erickson, A. W. 1977. Population studies of killer whales (*Orcinus orca*) in the Pacific Northwest: a radio-marking and tracking study of killer whales. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-285615, 34 p.

[8]Anonymous. 1977. The application of high purity carbon technology for Rehabilitation Engineering Center at Rancho Los Amigos Hospital. John F. Kennedy Space Center (NASA) Report SED-77-100, 146 p. Kennedy Space Center, Cape Kennedy, FL 32899.

[9]Cornell, L. H., E. D. Asper, K. Osborn, and M. J. White. 1979. Investigations on cryogenic marking procedures for marine mammals. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-291570, 24 p.

[10]J. G. Jennings, Fishery Biologist, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. October 1978.

[11]Shane, S. H., and D. J. Schmidly. 1978. Population biology of Atlantic bottlenose dolphin, *Tursiops truncatus*, in Aransas Pass, Texas. Available National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22151 as PB-283393, 130 p.

tags are most detectable, but are not durable and may damage the dorsal fin tissues. Freeze brands are durable, but not highly visible. Roto tags are of limited use for field identification except in unusual close range situations (e.g., Norris and Pryor 1970), although a combination color and location of the tag can identify an individual. For free-ranging dolphins, spaghetti tags are the only current tagging option, but identification of these tags usually requires collection of the animal. If animals are to be captured initially, combinations of tag types and use of natural marks can provide effective field identification.

Although radio tagging and tag or mark identifications are valuable tools for ecological studies of cetaceans, more development and testing of tags and attachment techniques are needed. Investigators should realize that tagging methods which are successful on one species may not work well on another species. Prior to field studies, tags should be tested on the species to be studied. We also recommend intensive follow-up sighting surveys to maximize data return and to determine the effect of tags and marks on free-ranging animals.

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NOTES

OFFSHORE WINTER MIGRATION OF THE ATLANTIC SILVERSIDE, *MENIDIA MENIDIA*[1]

The Atlantic silverside, *Menidia menidia*, is an abundant fish in coastal waters of the western Atlantic ranging from Florida to Nova Scotia. During spring, summer, and fall, the habitat of *M. menidia* includes intertidal creeks, marshes, and the shore zone of estuaries and embayments (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953). In such areas, ichthyofaunal surveys often cite *M. menidia* as the most numerous species encountered (Mulkana 1966; Richards and Castagna 1970; Chestmore et al. 1973; Briggs 1975; Anderson et al. 1977; Hillman et al. 1977). The entire life cycle of *M. menidia* is completed in 1 yr. Reproduction occurs in the spring, juveniles grow rapidly during the summer and reach full adult size by late fall. However, considerable uncertainty exists concerning winter ecology and habitat. In populations from Chesapeake Bay northward, Atlantic silversides are rare or absent from the shallow waters of the shore zone in midwinter (Warfel and Merriman 1944; Bayliff 1950; Hoff and Ibara 1977; Conover and Ross in press). Hildebrand and Schroeder (1928) and Richards and Castagna (1970) reported that *M. menidia* were captured in midwinter with bottom trawls in deepwater areas of Chesapeake Bay and deep estuarine channels in eastern Virginia. Catches of *M. menidia* have also been occasionally reported up to 15 km offshore (Clark et al. 1969; Fahay 1975). However, Needler (1940) noted that Atlantic silversides could be taken through the ice in Malpeque Bay, P.E.I. (although he presented no data concerning relative seasonal abundance), and investigations in South Carolina found an abundance of *M. menidia* in intertidal marsh creeks during winter (Cain and Dean 1976; Shenker and Dean 1979).

Because the Atlantic silverside is an important forage fish (Merriman 1941; Bayliff 1950; Bigelow and Schroeder 1953) and reaches a high level of biomass in the shore zone of marshes and estuaries (7.8 g/m^2 wet weight) (Conover and Ross in press), the winter movement patterns of this annual species could represent a significant pathway of energy flow from and/or within estuarine systems. This paper demonstrates that Atlantic silversides migrate offshore in winter, and we discuss aspects of their winter ecology and distribution by examining catch records of the bottom trawl survey program of the Northeast Fisheries Center (NEFC) of the National Marine Fisheries Service (NMFS).

Methods

A modern series of standardized bottom trawl surveys was begun in 1963 by the Bureau of Commercial Fisheries (BCF) Woods Hole Laboratory (Grosslein 1969). Initially, fall surveys encompassed the general range of offshore groundfish stocks of primary interest (i.e., gadoids) and thus was confined to the area between Hudson Canyon and Nova Scotia and depths from 27 to 366 m. Later, as the goals and emphasis of the survey program expanded to include a wider variety of species, both fall and spring surveys were conducted and the sampling area was extended southward to Cape Hatteras (1967). The offshore survey region was stratified into geographic zones based on depth contours and area (Grosslein 1969). A stratified random sampling design was employed to locate trawl stations within depth strata and the number of stations was allocated in proportion to stratum area. A standard No. 36 Yankee bottom trawl with a 1.25 cm stretched mesh cod end liner was towed at each station for 30 min at an average of 3.5 kn; however, spring offshore surveys since 1973 have used the larger No. 41 Yankee trawl. Stations were sampled continuously 24 h/d during cruises.

Synoptic bottom trawl surveys in the nearshore environment were begun in 1972 by the NMFS Sandy Hook Laboratory. Early surveys in the inshore region (defined as depth strata of 5-27 m) assessed the technical and geographic feasibility of using offshore sampling gear in waters as shallow as 5 m. Since autumn 1972, inshore surveys have been conducted each fall and spring with summer cruises added in 1977 and a winter cruise in 1978. Of 18 inshore cruises through 1978, most (17) included the region from

[1]Contribution No. 73 of the Massachusetts Cooperative Fishery Research Unit.

Cape Cod to Cape Hatteras, 4 included the Gulf of Maine, and 7 included the region from Cape Hatteras to Cape Fear. During 1972-75, all inshore surveys used either a ¾ modified Yankee trawl or the No. 36 Yankee trawl. Since 1976, a No. 41 Yankee trawl has been used. Towing procedures were the same as described for offshore surveys. The seasonal and geographic variation in the extent of inshore surveys reflects their evolution as a monitoring tool.

Capture data employed in this study included date, location, time, depth, surface and bottom temperatures, and number collected. Catch locations from all surveys were plotted to the nearest 10′ of latitude and longitude on depth contour maps by season. Surface and bottom temperatures and depth frequencies were plotted for each occasion that *M. menidia* were captured.

Results

Standard bottom trawl tows at 2,057 stations from inshore surveys collected 979 *M. menidia* at 107 sites (5.2% occurrence), while offshore tows at 10,209 stations captured 464 *M. menidia* at 72 sites (0.7% occurrence). Because sampling effort by season was not uniform with respect to inshore and offshore surveys or geographic zones, analysis of catch per effort data (catch frequency) was compiled by month for inshore and offshore surveys in three geographic regions (i.e., Gulf of Maine-Georges Bank, Cape Cod-Cape Hatteras, Cape Hatteras-Cape Fear). In the inshore surveys, effort was primarily concentrated in the Cape Cod-Cape Hatteras region, where the percent frequency of capture of *M. menidia* was negligible in summer, increased in November (4.9%), peaked in January (34.3%), and declined through the spring (Table 1). Number of stations sampled in the inshore surveys of the Gulf of Maine-Georges Bank and Cape Hatteras-Cape Fear regions was inadequate for monthly or regional comparisons. In offshore surveys, the monthly pattern of occurrence of *M. menidia* was similar to that of inshore surveys; catch frequency was zero in summer and autumn, peaked in January (3.8%) in the Gulf of Maine-Georges Bank and in February (11.2%) in the Cape Cod-Cape Hatteras regions, and declined thereafter (Table 2). These data support the hypothesis of an offshore winter migration.

The geographic distribution of catches by season (Fig. 1) indicates that most collections are confined to a zone within roughly 50 km of the shoreline and within the 40 m depth contour. One collection occurred 170 km from the mainland. Although most catches appear to occur between Cape Cod and Cape Hatteras and especially in the New York Bight, sampling effort among inshore surveys was much greater in this region as previously noted (Table 1). Although only four collections of *M. menidia* were observed south of Cape Hatteras (two off Cape Fear, S.C., and two off Cape Romain, S.C.; not appearing in Figure 1), no offshore or inshore surveys were conducted south of Cape Hatteras in winter when catches might be expected.

Surface temperatures recorded at 141 of the inshore and offshore stations where Atlantic silversides were captured ranged from 1° to 22°C, but 86% of these were within a range of 2°-6°C ($\bar{x}$ = 4.9°C; Fig. 2A). Bottom temperatures recorded at 135 collecting sites revealed a similar

TABLE 1.—Percent frequency of occurrence of *Menidia menidia* at stations sampled in the inshore survey region (depth strata of 5-27 m) of the NMFS bottom trawl survey program over the continental shelf of eastern North America. Catch statistics are from cruises conducted from 1972 to 1979 and are pooled by month and area of capture. The number in parentheses is the total number of stations sampled.

Month	Gulf of Maine and Georges Bank		Cape Cod-Cape Hatteras		Cape Hatteras-Cape Fear	
Jan.	—	(0)	34.3	(70)	0.0	(2)
Feb.	—	(0)	—	(0)	—	(0)
Mar.	—	(0)	21.4	(206)	0.0	(18)
Apr.	0.0	(7)	9.6	(240)	0.0	(25)
May	—	(0)	0.7	(141)	—	(0)
June	—	(0)	0.0	(33)	—	(0)
July	0.0	(3)	0.0	(41)	0.0	(47)
Aug.	0.0	(80)	0.5	(216)	0.0	(31)
Sept.	—	(0)	0.0	(150)	0.0	(82)
Oct.	—	(0)	0.2	(398)	0.0	(40)
Nov.	0.0	(10)	4.9	(183)	9.1	(22)
Dec.	—	(0)	0.0	(6)	33.3	(6)

TABLE 2.—Percent frequency of occurrence of *Menidia menidia* at stations sampled in the offshore survey region (depth strata 27-366 m) of the NMFS bottom trawl survey program over the continental shelf of eastern North America. Catch statistics are from cruises conducted from 1963 to 1979 and are pooled by month and area of capture. The number in parentheses is the total number of stations sampled.

Month	Gulf of Maine and Georges Bank		Cape Cod-Cape Hatteras		Cape Hatteras-Cape Fear	
Jan.	3.8	(159)	—	(0)	—	(0)
Feb.	0.4	(221)	11.2	(98)	—	(0)
Mar.	0.0	(386)	4.3	(925)	0.0	(18)
Apr.	0.2	(1,270)	1.5	(518)	—	(0)
May	0.0	(456)	0.0	(2)	—	(0)
June	—	(0)	—	(0)	—	(0)
July	0.0	(310)	0.0	(114)	0.0	(41)
Aug.	0.0	(522)	0.0	(336)	—	(0)
Sept.	—	(0)	0.0	(344)	0.0	(9)
Oct.	0.0	(1,265)	0.0	(1,219)	—	(0)
Nov.	0.0	(1,628)	0.0	(154)	—	(0)
Dec.	0.0	(155)	0.0	(55)	—	(0)

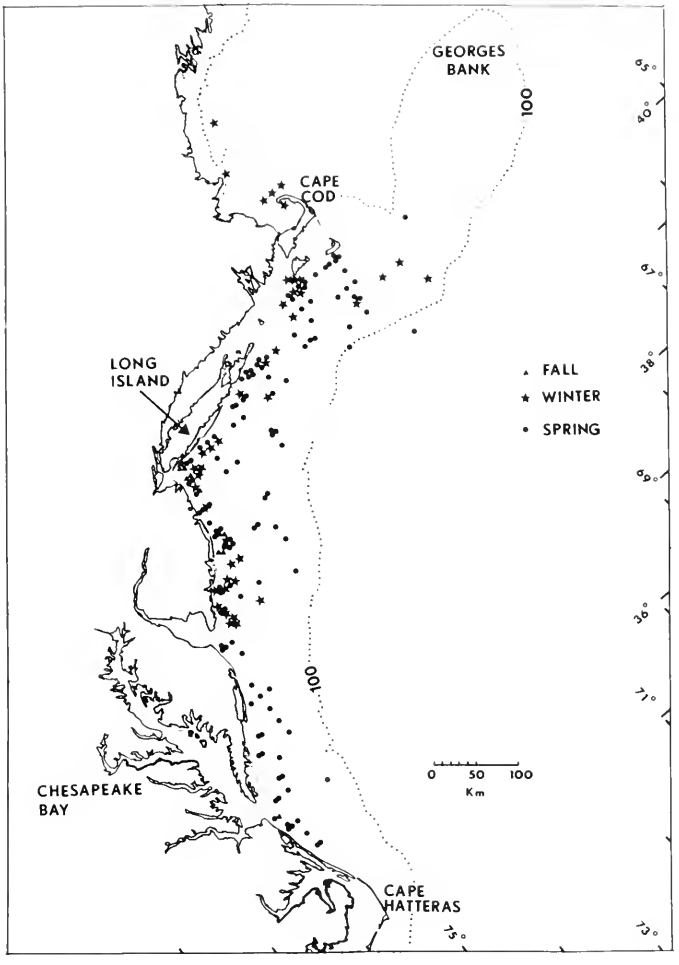

FIGURE 1.—Location of Atlantic silverside catches by season during inshore and offshore bottom trawl surveys of the National Marine Fisheries Service, Cape Hatteras to Nova Scotia, 1963-79 (fall = Sept.-Nov.; winter = Dec.-Feb.; spring = Mar.-May). Seven catch locations do not appear: Two off the northern coast of Maine, one off the outer coast of southern Nova Scotia, two off Cape Fear, S.C., and two off Cape Romain, S.C.

pattern: the majority (86%) of all Atlantic silverside collections occurred within a range of 2°-6° C ($\bar{x}$ = 5.1°C; Fig. 2B). These data indicate that *M. menidia* occur over the continental shelf primarily under winter temperature conditions after fall overturn when temperatures are isothermal.

The distribution of Atlantic silversides with respect to depth was examined by comparing catch frequency to depth of capture in 5 m intervals. The majority of catches occurred in waters <50 m deep (86%), and 42% of all catches were in depths of 10-20 m (Fig. 3). Maximum depth of capture was 126 m.

Some aspects of the winter ecology of Atlantic silversides while at sea can be revealed by examining their vertical distribution in the water column. Vertical distribution was inferred from diel variations in capture times partitioned into six 4-h intervals. Chi-square analysis comparing catch frequency in each time interval to all others combined showed that catch frequencies during night intervals (2000-0359 h) were significantly less than expected ($P<0.01$; Table 3), while catch frequencies during midday intervals (0800-1559 h) were significantly greater than expected ($P<0.01$). Apparently, *M. menidia* occurred nearer the bottom during daylight hours and hence were more susceptible to bottom trawl tows conducted during the day. These observations indicate that while at sea, Atlantic silversides are vertical migrators like other planktivores such as Atlantic herring, *Clupea harengus*, (Blaxter 1975) and American shad, *Alosa sapidissima*, (Neves and Depres 1979).

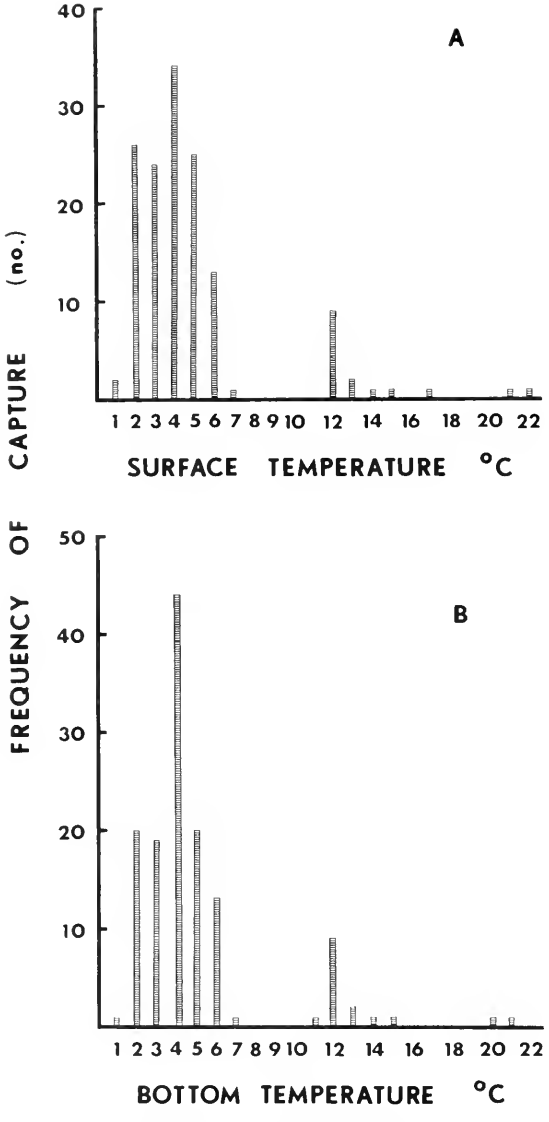

FIGURE 2.—Water temperatures at stations where Atlantic silversides were captured during inshore and offshore bottom trawl surveys conducted by the National Marine Fisheries Service during 1963-79 over the eastern North American continental shelf. A. Surface temperatures (n = 141). B. Bottom temperatures (n = 135).

Discussion

The results of this study demonstrate that populations of *M. menidia* north of Cape Hatteras undergo an offshore winter migration from inland to inner continental shelf waters. Atlantic silverside winter habitat probably also includes

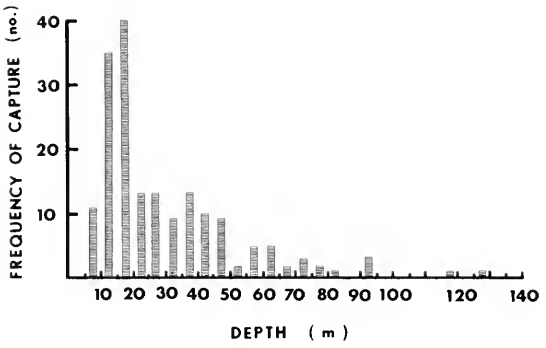

FIGURE 3.—Water depths at which Atlantic silversides were captured during inshore and offshore bottom trawl surveys of the National Marine Fisheries Service over the eastern North American continental shelf, 1963-79.

TABLE 3.—Chi-square analysis of diel variations in catch frequencies of Atlantic silversides in combined inshore (5-27 m) and offshore (27-366 m) trawl surveys conducted by NMFS, 1963-79, over the continental shelf of eastern North America.

Time of capture (e.s.t.)	Tows capturing *Menidia* (no.)		χ^2
	Observed	Expected	
0000-0359	11	29.8	14.3***
0400-0759	28	29.8	0.1
0800-1159	46	29.8	10.5***
1200-1559	43	29.8	7.0**
1600-1959	35	29.8	1.1
2000-2359	16	29.8	7.7**
Totals	179	179	

** $P<0.01$.
*** $P<0.005$.

deep inland waters not sampled by NMFS surveys, as Hildebrand and Schroeder (1928) and Richards and Castagna (1970) have noted. Since the lower lethal temperature for *M. menidia* in short-term experiments was 1°-2°C (Hoff and Westman 1966; Conover unpubl. data), the offshore migration may be promoted by potentially stressful or lethal low water temperatures in shallow inland waters during midwinter. Conover and Ross (in press) and Warfel and Merriman (1944) found that Atlantic silversides leave the New England shore zone in November as water temperatures drop to about 6°-8°C. The timing of Atlantic silverside disappearance from shallow inland waters corresponds closely with their appearance in deeper offshore waters.

If the offshore migration of Atlantic silversides is primarily motivated by low temperature stress, than offshore movements in warmer waters, such as south of Cape Hatteras, would not be expected. Even though our data cannot

address this question directly, evidence from ichthyofaunal surveys in South Carolina indicate that *M. menidia* abundance remains high in intertidal creeks (Cain and Dean 1976; Shenker and Dean 1979) and in the surf zone of barrier beaches (Anderson et al. 1977) throughout winter.

The relative abundance of Atlantic silversides over the continental shelf is difficult to judge from this study, since bottom trawling is a relatively ineffective method for catching small pelagic fish such as *M. menidia* (see Conover and Ross in press). In addition, the low overall catch frequency for *M. menidia* reported herein is primarily due to the relatively small number of stations sampled in midwinter when maximum catches might be expected. Neves and Depres (1979) used similar NMFS offshore survey data on a larger pelagic species, the American shad, and reported catches at 527 of the 10,435 stations sampled (5.05%). Considering the methods used, the percent occurrences of *M. menidia* in the inshore and offshore surveys of the mid-Atlantic during midwinter (34 and 11%, respectively) may indicate considerable abundance.

In a previous study, Conover and Ross (in press) showed that Atlantic silversides reach a high level of biomass during late fall in marsh areas and also suffer a high rate of winter mortality (90-99%). Their hypothesis that winter movement and mortality patterns of *M. menidia* represent a one-way export of biomass from the shore zone of bays, marshes, and estuaries to offshore communities is strengthened by this study. The causes of high winter mortality experienced by Atlantic silversides at northern latitudes are unknown but conceivably could include predation and perhaps physiological stress imposed by the migration itself and prolonged exposure to cold temperatures. Atlantic silversides could be an important forage fish over the inner continental shelf, but it will require an analysis of the food habits of offshore fishes in midwinter to address this question.

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GROWTH DURING METAMORPHOSIS OF ENGLISH SOLE, *PAROPHRYS VETULUS*

Among fishes, the period of transformation from the larval to adult form is marked not only by changes in morphology, behavior and in some species, habitat (Jakóbczyk 1965; Sale 1969; Hoar 1976; Marliave 1977), but in growth rate as well. Ontogenetic changes in growth have not been well documented principally because a method for determining age of larvae and juveniles has not, until recently, been available. The discovery of daily growth rings on otoliths has made possible the precise determination of age, in days, of larval and juvenile fishes (Brothers et al. 1976). Changes in growth rates during different life history stages which could be correlated with behavioral and habitat changes were observed in the French grunt, *Haemulon flavolineatum* (Brothers and MacFarland in press). Struhsaker and Uchiyama (1976) observed an inflection point in the age-length plot of larval and juvenile nehu, *Stolephorus purpureus*, indicating a change in growth rate. This inflection point corresponded with the size when body depth began to increase in proportion to the length of the fish, but not with changes in diet or habitat that occur over the course of development.

Age estimates based on counts of otolith growth increments have now allowed us to determine growth during metamorphosis of the pleuronectid *Parophrys vetulus* Girard.

Methods

The results of this study are based on the standard length (SL) in millimeters and age in days of 127 pelagic larvae and transforming individuals of *P. vetulus* ranging 10-20 mm SL, and 106 benthic 0-age individuals from 18 to 35 mm SL. Pelagic specimens were collected off Newport, Oreg. (approximately lat. 44°37′N, long. 124°06′ W), from November 1977 through June 1978 with a 70 cm bongo net with 0.505 mm Nitex[1] mesh (see Laroche et al. 1982 for sampling details). Benthic *P. vetulus* were collected off Moolach Beach, Oreg., 10 km north of Newport, during September 1978 through September 1979 with a 1.5 m wide beam trawl (7 mm stretch mesh).

The removal and mounting of saccular otoliths from larvae followed the methods outlined in Methot and Kramer (1979) except that otoliths were mounted on rectangular glass cover slips to improve the optical properties of the preparation. Otolith growth increments were counted at 800 or 1250 × under bright-field illumination. A complete description of the counting technique and validation of the daily periodicity of the rings can be found in Laroche et al. (1982).

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

Otoliths from the benthic individuals were removed, mounted on glass microscope slides and ground to a sagittal thin section through the nucleus using 600 grit carborundum paper. Increment counts on these ground sections were made at 250-400 × using either bright-field or polarized illumination.

The age of each fish was defined as the number of daily otolith growth increments plus five, the age at first increment formation for this species (Laroche et al. 1982).

In order to characterize changes in body form during metamorphosis, body depth, snout to anus length, lower jaw length, and the distance of migration of the left eye, of 65 larvae and 0-age benthic specimens were measured to the nearest 0.1 mm.

Results and Discussion

A plot of the length-at-age of *P. vetulus* larvae and juveniles taken in both pelagic and benthic collections exhibits a prominent plateau between 60 and 120 d of age and between 18 and 22 mm SL (Fig. 1). This plateau shows that there is a period of reduced growth in body length when these fish are undergoing metamorphosis. Plots of body depth and snout to anus length versus standard length both have a well-defined inflection point between 18 and 22 mm SL (Figs. 2, 3). Other morphometric measurement plots (lower jaw length and distance of migration of the left eye) (not shown) also contain an inflection between 18 and 22 mm SL, but less clearly. Changes in body morphology during the growth plateau are illustrated by examining a developmental series just prior to metamorphosis (Fig. 4A) and comparing individuals of similar sizes within the plateau (Fig. 4B). Changes in body depth are most pronounced, but eye migration and changes in head morphology are also evident.

The definition of two distinct growth stanzas separated by a plateau conforms to several of the criteria outlined by Ricker (1979). However, as he points out, the timing of the inflection points on the size-at-age plot depends on whether length or weight is measured. We have not measured weight in this study.

Due to the shape of the length-at-age plot we might expect the length-weight relationship for this species to be complex in form over the interval considered here.

The age of 18-20 mm SL *P. vetulus*, taken in plankton samples, was 41-74 d (about 1.4-2.4 mo) and those caught by the beam trawl, 49-116 d (about 1.6-3.9 mo; Fig. 1). The exact duration of transformation cannot be determined because of this large range. This is also illustrated by Figure 4B. The range in age of 11 pelagic specimens, 17.6-20.0 mm SL, whose left eye had begun migration, but was still on the left side of the body, was 49 d. However, if resumption of growth in body length is used to mark the end of metamor-

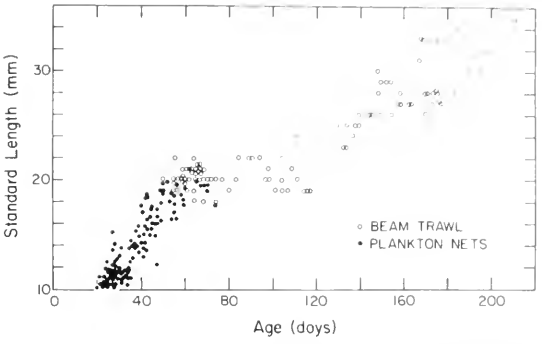

FIGURE 1.—Standard length versus age of *Parophrys vetulus* larvae and juveniles caught in plankton net and beam trawl collections.

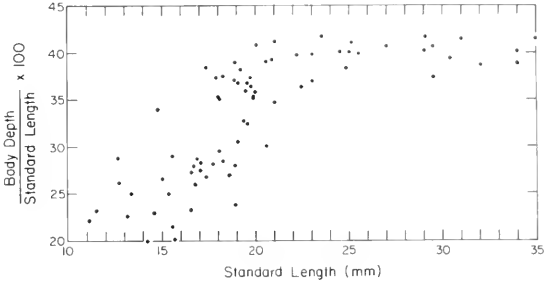

FIGURE 2.—Body depth as a percentage of standard length versus standard length of *Parophrys vetulus*.

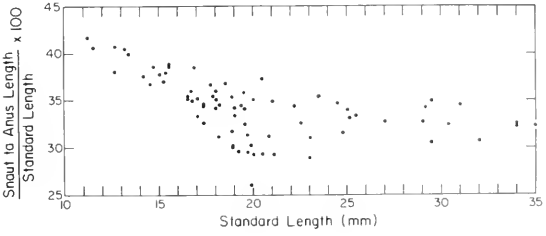

FIGURE 3.—Snout to anus length as a percentage of standard length versus standard length of *Parophrys vetulus*.

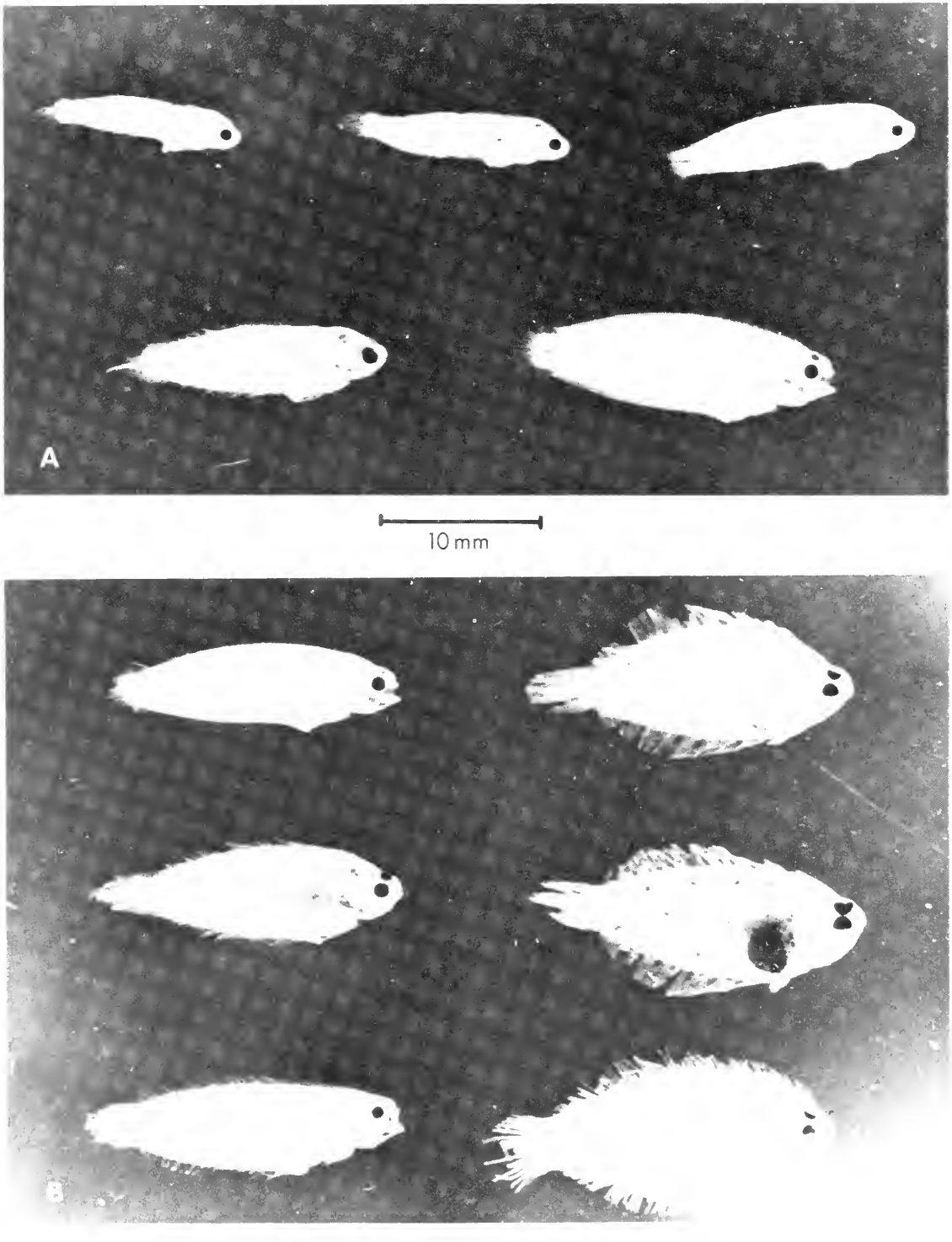

FIGURE 4.—A. Developmental series of *Parophrys vetulus* larvae. Top row, left to right, 11, 13, 14.9 mm SL; bottom 17, 19 mm SL. B. Pairs of *Parophrys vetulus* of similar lengths in different states of transformation. Top 18.0, 18.0 mm SL; middle 19.0, 19.1 mm SL; bottom 19.9, 20.0 mm SL.

phosis, then most *P. vetulus* had completed transformation by about 120 d old or 4 mo. The influence of substrate and water depth on rate of transformation in this species could be clarified only with laboratory experiments. A detailed description of body morphology versus age, as opposed to length would yield useful information on the variability in the timing of transformation. Unfortunately, we do not have such data.

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OBSERVATIONS ON LARGE WHITE SHARKS, *CARCHARODON CARCHARIAS*, OFF LONG ISLAND, NEW YORK

Fishermen report sightings of large white sharks, *Carcharodon carcharias*, off Long Island and southern New England every year. A popular book on shark fishing (Mundus and Wisner 1971), reported encounters with 23 large white sharks between 1958 and 1966 off Montauk Point, N.Y. Five of these were landed and weighed or estimated to range from 660 to 2,025 kg. Bigelow and Schroeder (1948) noted the occurrence of a few white sharks in southern New England waters. Otherwise most documented captures of white sharks off eastern North America are from coastal locations north of Cape Cod, Mass. (Schroeder 1938, 1939; Bigelow and Schroeder 1948, 1953, 1958; Scattergood et al. 1951; Scattergood and Coffin 1957; Scattergood and Goggins 1958; Scattergood 1959, 1962; Skud 1962; Templeman 1963; Arnold 1972). Information in these reports is limited to location sightings and morphometric observations.

We report here our detailed examinations of two white sharks landed off Long Island, N.Y., in 1964 and 1979. We also describe the feeding behavior of white sharks that were near a dead fin whale, *Balaenoptera physalus*.

Material Examined

One of us (J. G. Casey) caught a 406 cm TL (total length) immature female white shark on rod and reel 7.2 km south of Amagansett, N.Y., (lat. 40°53′ N, long. 72°06′ W) on 5 October 1964. When landed, its stomach was everted. Weight was estimated at 1,500 lb (680 kg) and morphometric measurements were taken to the nearest millimeter.

On 29 June 1979 Captain Thomas Cashman from the charter boat *Rogue* harpooned a male white shark (457 cm TL) while it fed on a 14-15 m dead and floating fin whale 24 km southwest of Moriches Inlet, N.Y., (lat. 40°32′ N, long. 72°50′ W) in 35-40 m of water. The white shark landed at Center Moriches, N.Y., weighed 2,075 lb (943 kg). The following morning we photographed, measured, and dissected the specimen. Morphometric measurements for both specimens (Table 1) follow the conventions of Bigelow and Schroeder (1948).

Biological Observations

Maturity.—The male white shark was sexually mature judging from the condition of the 40 cm claspers (Clark and von Schmidt 1965). The well-developed testes and spermatophores in the lower ductus deferens (Pratt 1979) provided additional evidence of fecund male maturity. The female was immature judging from the small size of the oviducts (approximately 1 cm in diameter).

TABLE 1.—Morphometric measurements of body parts with proportional dimensions as percent of total length.

Body part	1964 female		1979 male	
	cm[1]	% of TL	cm	% of TL
Total length	[1]406.4	100	457	100
Fork length	[2]375.9	92.5	425	93
Distance from snout to:				
eyes	27.9	6.9	27	5.9
nostrils	16.5	4.1	18	3.9
mouth	25.4	6.3	—	—
first gill (base)	99.1	24.4	100	21.9
pectoral	106.7	26.3	126	27.6
first dorsal	154.3	38.0	179	39.2
second dorsal	—	—	334	73.1
pelvic	—	—	277	60.6
anal	—	—	347.5	76.0
upper caudal pit	335.9	82.7	389	85.1
Interspace between:				
1st and 2d dorsal	99.1	24.4	110.5	24.2
2d dorsal and caudal	38.1	9.4	57	12.5
pelvic and anal	43.8	10.8	58.3	12.8
anal and caudal	30.5	7.5	43	9.4
nostrils (proximal)	19.1	4.7	20.3	4.4
Height of:				
1st dorsal	45.1	11.1	43.5	9.5
free tip	11.4	2.8	10.3	2.3
2d dorsal	7.0	1.7	6.5	1.4
free tip	8.9	2.2	7.8	1.7
Diameter of eye:				
horizontal	3.8	.9	3.5	.8
vertical	—	—	4.5	1.0
Right clasper	—	—	40.4	8.8
Left clasper	—	—	40.5	8.9
Width of mouth	43.2	10.6	37.5	8.2
Height of mouth	24.1	5.9	—	—
Max length pectoral fin	78.7	19.4	76	16.6
Girth	218	53.8	260	47.7
Weight, kg	[3]680	—	943	—

[1]Female measured in inches and converted.
[2]Calculated from total length using 92.5% (mean derived from author's unpubl. data).
[3]Estimate.

Stomach Contents and Liver.—The male's stomach and its contents weighed 52 kg when separated at the esophagus. Fifteen "bite-sized" pieces of whale blubber and muscle, 18-60 cm in diameter, in the stomach weighed 28 kg. The largest piece measured 60 × 30 × 10 cm. The stomach, distended and taut, appeared filled nearly to capacity. The liver was large, light-colored, and robust. Both lobes together weighed 178.9 kg.

Parasites.—Circumstances did not permit an exhaustive search for parasites; however, one copepod species, *Dinemoura latifolia*, was collected from the lateral surface of the caudal fin of the male.

Behavior.—One of us (R. B. Conklin) observed at least four and possibly as many as nine white sharks intermittently for 30 h (28-29 June 1979) in the vicinity of the dead fin whale. No more than two ever occurred together, and these appeared agonistic. On one occasion a 3-4 m white shark with a tooth slash over the gills approached the fin whale, then quickly changed direction and disappeared without feeding. This may have been an evasive action because seconds later a much larger male (5-6 m) appeared in the same place and began feeding on the fin whale. Some of the white sharks observed around the fin whale, including the harpooned male, had either fresh or healed tooth slashes on their sides, between the gills and caudal peduncle. These are probably not the mating cuts reported for other shark species (Stevens 1974; Pratt 1979), since they occurred on males and immature females. The tooth slashes and cuts observed on these white sharks are most likely inflicted on co-specifics while competing for prey.

Feeding behavior was observed on four occasions and probably involved different sharks. In three of the four contacts the white shark rolled and attacked with its ventral surface up (Figure 1). After the teeth were in the fin whale carcass, the white shark rolled upright thrashing its tail and cleanly cut away a mouthful of blubber. This behavior was characteristic of attacks on intact parts of the fin whale near the waterline. On the fourth occasion the white shark fed in an upright swimming position, biting on a broad piece of floating flesh.

Fishermen and film makers visited the fin whale each day from 1 to 6 July to observe and photograph the white sharks. Each morning a

FIGURE 1.—A 4 m male white shark rolling ventral side up to feed on the tail section of a dead 14-15 m fin whale. The white shark's head is under the fin whale toward the right.

white shark of 4-5 m appeared within minutes of the boat's arrival and patrolled or fed for 10-15 min. The observers believed that three to six different white sharks fed on the fin whale during this week; however, only one white shark was observed patroling and feeding at any one time after the initial discovery.

On 6 July 1979, two of us (H. L. Pratt and J. G. Casey) visited the whale carcass, which was in an advanced state of decay. A 4.5 m white shark soon appeared after the boat arrived at the fin whale. The white shark slowly circled the boat and the fin whale, then disappeared. It returned and repeated this behavior at 2-4 h intervals occasionally feeding on the fin whale.

Although the blue shark, *Prionace glauca*; shortfin mako, *Isurus oxyrinchus*; and other pelagic sharks are abundant in this area in July, they were conspicuously absent from the vicinity of the fin whale carcass. Blue sharks were being caught 5-10 km away from the fin whale. Ken Grimshaw, an experienced fish spotter pilot, made several flights over the area, and saw no blue sharks or fish schools within a 3.2 km radius of the whale. It is not unusual for fishermen to report poor catches just prior to a white shark sighting. We suggest that in these cases, the white sharks territorially exclude other species from the area.

Strength.—Based on the amount of time and size of tackle needed to land a large white shark, its strength assumes heroic proportions. The harpoon dart entered the body cavity of the 457 cm white shark forward and below the right pectoral fin, pierced the stomach and lodged in a 5 kg piece of whale blubber. The white shark then towed a 29 l keg and 26-30 m of 9.5 mm nylon line for 14½ h. Nine of these hours were spent with added resistance from the boat through 80-lb test fishing gear attached to the keg. In its final dive, it pulled a heavy nylon line out of the hands of four men. In a similar situation in June 1978, a white shark reported to be 10 m long towed Captain John Sweetman's 42-ft (12.8 m) charterboat backwards a distance of 22 km in 13 h before breaking free (Simons 1978).

Discussion

The occurrence of large white sharks in the shelf waters of the New York Bight is a well established, though often overlooked, fact. Difficulty in observing, field-identifying, and catching white sharks has resulted in a poor understanding of their presence and numbers. Their occurrence in these shelf waters may be related solely to feeding habits; however, it may also be related to reproductive activity. Judging from newspaper and other photographs, most of the large white sharks in this area are females that are approaching maturity (3-4 m FL) or are mature (4-5 m FL). At least three mature males were attracted to the dead fin whale. The presence of mature individuals of both sexes suggests that these offshore waters may be a seasonal mating ground for the white shark.

The presence of young (118-150 cm FL) white sharks in coastal waters of the New York Bight (Casey and Pratt unpubl. manuscr.) and the presence of very large females suggests that pupping may occur here or enroute during the spring migration.

Documentation in popular literature (Baldridge 1974; Ellis 1975) and commercial motion picture films indicate that white sharks attack in

an upright position. The rolling behavior reported here may be a specific pattern for feeding on large flat or slightly convex surfaces (i.e., flanks of whales).

White sharks are known to prey on seals and porpoises (Fitch 1949; Arnold 1972). Records of predation on whales are sparse and usually cited in personal communications (Randall 1973). Calculations of the energy requirements of white sharks (Carey et al. 1979), suggested that dead whales may be a primary food source for white shark populations in the western North Atlantic.

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A NOTE ON THE ESTIMATION OF TRIMETHYLAMINE IN FISH MUSCLE

The chemical methods for estimation of trimethylamine (TMA) in fish muscle consist of: 1) making a protein-free extract of tissue, 2) treating with formaldehyde (FA) to fix ammonia and amines other than tertiary amines, 3) volatilizing TMA with alkali into an organic phase (toluene), and 4) measuring the degree of ionization of picric acid in toluene caused by the extracted amine.

The methods have caused controversy; they have varied in detail such that the results from different laboratories have not always been in agreement (Shewan et al. 1971).

Bullard and Collins (1980) have recently compared methods of analysis for TMA and the interference by ammonia and dimethylamine (DMA). They included the method of Murray and Gibson (1972a) and confirm that 45% KOH as alkali is optimal for the release of TMA into the organic phase. They showed that the recovery of DMA is higher than is acceptable and that DMA interferes with the assays for TMA. Murray and Gibson (1972b) had found that the interference was very low and insignificant.

Tozawa et al. (1971) showed that the concentration of FA was critical in order to minimize the interference from DMA (see their fig. 3). They found that 0.5-1.0 ml FA was optimal for a 4 ml sample and added the FA before the toluene. If less were added, significant interference from DMA occurred even with KOH as alkali rather than K_2CO_3.

Bullard and Collins (1980) added only 1 ml of 3.7% FA to the sample (4 ml) after the addition of toluene. FA and aqueous FA, which exists as methylene glycol, are soluble in toluene and thus the effective concentration of FA in the aqueous sample is probably much lower than the minimum recommended by Tozawa et al. (1971) and is in the range which would cause maximum interference by DMA.

Murray and Gibson (1972a) used 1 ml of 50% neutralized FA added before toluene. They compared their procedure with that of Tozawa et al. (1971) and found no significant differences (unpubl. results). In addition they examined chromatographically the toluene phase after extraction and found that in their procedure only TMA was extracted (Murray and Gibson 1972b).

Thus it would have been more realistic and fair to previous workers if Bullard and Collins (1980) had compared the actual published methods rather than their modifications to them and if they had specifically analyzed the material extracted into the toluene fraction. Accordingly their claim to have improved the method for TMA analysis cannot be substantiated.

It would be interesting to compare the results of analysis of samples from different species using the actual published methods done by an independent laboratory.

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SNOUT DIMORPHISM IN WHITE STURGEON, *ACIPENSER TRANSMONTANUS*, FROM THE COLUMBIA RIVER AT HANFORD, WASHINGTON

Several publications (Bajkov 1951; Semakula 1963; Vladykov and Greeley 1963; Semakula and Larkin 1968; Haynes et al. 1978; Haynes and Gray 1981) describe the behavior, natural history, and taxonomy of white sturgeon, *Acipenser transmontanus*. Although differences in snout length and shape between young and adult white sturgeon are known, morphological divergence in snout type of similar sized individuals has not been reported. We observed and documented a morphological dimorphism in the snouts of juvenile and adult white sturgeon in the Hanford reach of the Columbia River.

Materials and Methods

Sturgeon were collected in April and June 1977 with 100 m trammel nets at White Bluffs Pool (River Mile 371) on the Columbia River. Specimens were examined in the field, and total length (TL), physical characteristics, and snout types were recorded. A subsample of 10 sturgeon (41-92 cm TL), 5 designated "long snout" and 5 "short snout," was taken to the laboratory where detailed snout and head measurements were made and sex was determined (these fish were <100 cm TL to facilitate storage). All other fish were released after examination. Morphometric and meristic measurements followed Hubbs and Lagler (1958). A discriminate analysis (Morrison 1976) was used to select separating characteristics.

Results and Discussion

Field observations on 99 white sturgeon ranging from 35 to 205 cm TL showed two snout types based on size and shape. Although both snout types fit the basic characteristics of white sturgeon summarized in Scott and Crossman (1973), the short snout specimens captured at White Bluffs were more representative of that description: "...snout in adults short, depressed, bluntly rounded, shorter than postorbital length, in young sharper, longer than postorbital length; ...." The long snout was morphologically similar except for a long, slender, and pointed snout. The long snout characteristic was more pronounced in smaller immature fish measuring 35-120 cm TL, but was still evident in larger more mature individuals (Figs. 1, 2). Of the sampled population, 48% exhibited the long snout and 47% the short snout characteristics, and 5% could not be identified with either group.

Mean total length of white sturgeon examined in the laboratory was 65.50±20.63 cm for long snout and 70.62±18.79 cm for short snout fish (mean snout lengths were 6.77±1.65 cm and 6.58±0.91 cm, respectively). Of 21 morphometric and meristic measurements made on the subsample, 6 were deemed appropriate to demonstrate snout differences (Table 1). Although sample size was small, the data suggest a correlation between snout length and sex. Of the 10 sturgeon examined in the laboratory, all long snout specimens were males while 4 of 5 short snout specimens were females.

Snout type differences in white sturgeon have not been reported in other areas of the species range. The occurrence of this dimorphism at Hanford may reflect isolating mechanisms, such as physical barriers which block white sturgeon movements. Bajkov (1951) suggested that hydroelectric dams along the Columbia River isolate white sturgeon populations, preclude immigration and lead to divergent evolution. White Bluffs Pool is in the Hanford reach of the Columbia River which is bounded upstream by Priest Rapids Dam and downstream by McNary Dam. The adaptive significance of this dimorphism at Hanford is unknown.

TABLE 1.—Measurements used to demonstrate differences between five long snout and five five short snout white sturgeon.

	Long snout			Short snout		
Characteristic	Mean	SD	Range	Mean	SD	Range
Total length, cm	65.50	20.63	41.90-92.00	70.62	18.79	49.40-91.50
Head length, cm	15.13	4.03	10.30-20.95	15.59	4.00	10.70-19.35
Snout length, cm	6.77	1.65	5.05- 9.50	6.58	.91	5.50-12.50
Barbles to rostrum (B-R) ratio	4.34	.95	3.20- 5.80	3.40	.44	2.30- 3.50
Head length/snout length	2.23	.20	2.04- 2.52	2.37	.30	1.96- 2.70
Snout length/total length, %	10.34	1.71	7.62-12.18	9.32	1.46	8.98-12.20
B-R/total length, %	6.63	.87	5.50- 7.64	4.81	.95	3.50- 5.84

FIGURE 1.—Juvenile (above) and older (below) white sturgeon showing long (LS) and short (SS) snout characteristics.

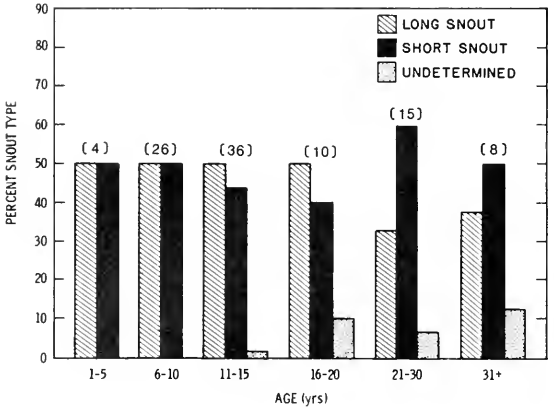

FIGURE 2.—Distribution of snout type with age for white sturgeon, *Acipenser transmontanus*, at Hanford. Age class was estimated from length based on data from Semakula (1963) for the Fraser River. Sample size in each age class in parentheses.

Acknowledgments

We thank C. D. Becker, who critically reviewed the manuscript, J. M. Haynes, and J. C. Montgomery who assisted data collection in the field, and R. L. Bushbom for statistical analysis. The study was supported by the U.S. Department of Energy under Contract EY-76-C-06-1830 with Battelle Memorial Institute, Pacific Northwest Laboratory.

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Vol. 80, No. 2 April 1982

(Continued on back cover)

Seattle, Washington

Fishery Bulletin

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

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Seattle, Washington

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Notes

Notices

DEVELOPMENT OF THE VERTEBRAL COLUMN, FINS AND FIN SUPPORTS, BRANCHIOSTEGAL RAYS, AND SQUAMATION IN THE SWORDFISH, *XIPHIAS GLADIUS*[1]

THOMAS POTTHOFF AND SHARON KELLEY[2]

ABSTRACT

The development and structure of the fins and their supports, of the vertebral column, and the scales are described from 220 cleared and stained *Xiphias gladius*. Details on development and structure of the pectoral fin, the pectoral suspensorium, and the coraco-scapular cartilage are given. The pectoral suspensorium in *Xiphias* is slightly reduced; only one postcleithrum is present and intertemporals are absent. A cartilaginous distal radial was observed between the base of the dorsalmost pectoral ray during development. Dorsal and anal fin ray and pterygiophore development and structure are described. The anteriormost dorsal pterygiophore inserts in the second interneural space and originates from one and sometimes from two pieces of cartilage. The first anal pterygiophore inserts in the 16th interhaemal space and also originates from one but rarely from two pieces of cartilage. The posteriormost dorsal and anal pterygiophores insert in the 22d and 21st interneural-interhaemal spaces and have a stay and a serially associated double ray. Middle radials are absent in *Xiphias*. Details on hypural complex development and structure are given. *Xiphias* does not develop all basic perciform caudal complex parts. Missing are the centrum (PU_3) which has an autogenous haemal spine and a neural spine with articular cartilage, and the second (postero-dorsal) uroneural pair. All other basic perciform caudal complex parts are present but some fuse during development; e.g., hypurals 1-4 fuse with each other and with the urostyle to form a plate. The three epurals, the first (anteroventral) uroneural pair, hypural 5, the parhypural, and one haemal spine remain autogenous in adults. The development of the vertebral column and the structure of the vertebrae are described in detail. The ribs in *Xiphias* are unusual because generally only one pair is present on centra 1-5, 15, and 16. Centra 6-14 usually have no ribs. Ribs in *Xiphias* develop from cartilage. Branchiostegal ray numbers are variable in *Xiphias*. There may be seven rays on both sides, or seven on one side and eight rays on the other, or there may be eight rays on both sides. The development of squamation is described. Two types of scales develop: large row scales in four parallel rows and smaller scatter scales between rows. All scales develop from one to seven posteriorly recurved spines. Our largest 668 mm ESL specimen was covered with scales, but the recurved spines had become blunt and scatter scales could not be distinguished from row scales anymore.

The development and structure of the fins and fin supports for the swordfish *Xiphias gladius* have not been described in the literature. The skull and vertebrae of adult *Xiphias* were studied by Gregory and Conrad (1937) and Nakamura et al. (1968) and brief description of vertebrae in adult *Xiphias* was given by Ovchinnikov (1970). Arata (1954) described the larvae and juveniles, and Yasuda et al. (1978) described embryonic and early larval stages. The purpose of this study is to document the development and anatomy of the fins and fin supports and vertebral column to afford comparisons of *Xiphias* with other fishes and to facilitate its phylogenetic placement. Although literature is abundant on larvae, juveniles, and adults of this monotypic species and genus (Palko et al. 1981), detailed osteological studies of *Xiphias* do not exist.

MATERIAL AND METHODS

The larvae and juveniles of *Xiphias gladius* were identified before clearing and staining according to the descriptions by Ehrenbaum (1905), Sanzo (1910, 1922), Regan (1924), Nakamura et al. (1951), Yabe (1951), Arata (1954), Tåning (1955), Jones (1958, 1962), Yabe et al. (1959), Markle (1974), and Yasuda et al. (1978). There were no identification problems (Richards 1974).

Cleared and stained larvae before and during notochord flexion were measured from the

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anterior orbit of the eye to the tip of the notochord (ENL) and those after notochord flexion were measured from the anterior orbit of the eye to the posteriormost edge of the hypural bones (ESL). The measurements were taken to the nearest 0.1 mm with a calibrated ocular micrometer for specimens <20 mm ESL, and for those >20 mm ESL, dial calipers were used. The reason for using ENL and ESL rather than standard length (SL) was that in most specimens the sword (bill) was damaged and standard length measurement would have been inaccurate.

A series of 220 *Xiphias gladius* from 3.7 mm ENL to 668 mm ESL captured with plankton nets, or by night light and dip netting, or taken from dolphin fish, *Coryphaena hippurus*, stomachs were cleared and stained for cartilage and bone by a combined method after Taylor (1967) and Dingerkus and Uhler (1977). Measurements of the specimens were taken after clearing and staining, because almost all *Xiphias* were twisted before clearing but were easily straightened after the clearing.

Although we had many smaller sized *Xiphias* larvae, we could have used more juveniles for our study (Fig. 1). Most of our specimens were collected in the Gulf of Mexico but a few were caught in the Caribbean Sea and Atlantic Ocean (Fig. 2).

All specimens were examined in 100% glycerin and under 100× to 150× magnification with a high-quality binocular dissecting microscope. Cartilage was viewed with the help of alcian blue stain, but cartilaginous structures that sometimes stained weakly or not at all were viewed by manipulating light intensity and the angle of the substage mirror. Onset of ossification was determined by light (pink) alizarin uptake, usually around the margin of a structure. Illustrations were drawn with the help of a camera lucida.

The osteological terms used in this study follow those used by Gosline (1961a, b), Nybelin (1963), Gibbs and Collette (1967), Monod (1968), and Potthoff (1975, 1980).

Counts of pterygiophores and fin rays include very small vestigial structures.

PECTORAL FIN

The pectoral fin rays in *Xiphias* were the first of all fin rays to begin development. The first rays were present at 4.8-5.6 mm ENL (Tables 1, 2). Development of the rays started on the dorsal border of the larval fin blade and proceeded in a

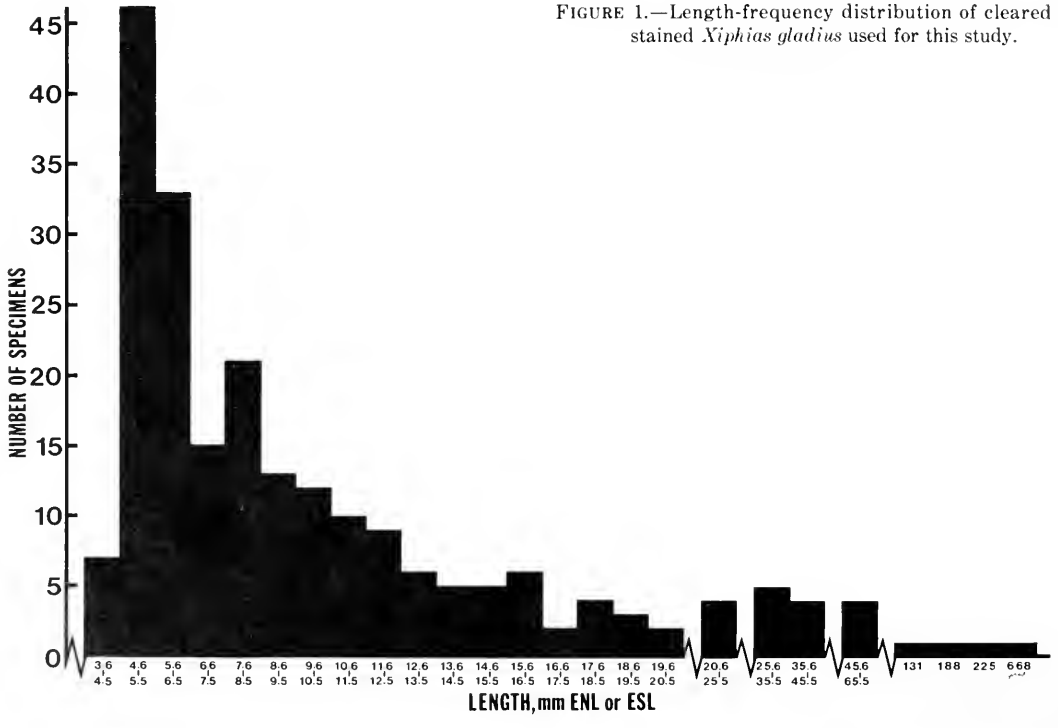


FIGURE 1.—Length-frequency distribution of cleared and stained *Xiphias gladius* used for this study.

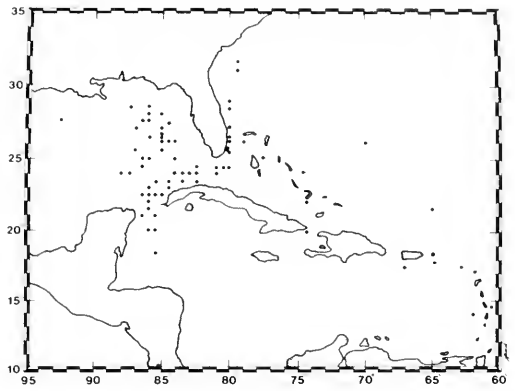


FIGURE 2.—Capture localities (black dots) of larval and juvenile *Xiphias gladius* used in this study. A locality may represent more than one capture.

TABLE 1.—Summary of fin development sequence in cleared and stained larvae of *Xiphias gladius*. PRC = principal caudal rays, SCR = secondary caudal rays.

Fin	Length ENL or ESL (mm)			Number of rays in fully developed fin
	First appearance of rays	All specimens have rays	Full complement of rays	
Caudal	5.4	6.1	26.7	34-38
PCR	5.4	6.1	8.8-11.0	17
SCR	7.8	11.6	26.7	8-10 dorsal 8-11 ventral
Dorsal fin	5.5	6.1	8.1-13.9	44-49
Anal fin	5.3	6.1	7.8-10.6	16-19
Pectoral fin	4.8	5.6	14.2-19.6	16-19

ventral direction. Adult counts of 16-19 rays were first obtained at 13.3 mm ESL and all specimens >19.5 mm ESL had the adult count (N = 20, $\bar{X}$ = 17.6, SD = 0.89) (Table 2).

Pectoral fin ray counts differed for individual specimens between sides. Of 154 specimens 4.6 mm ENL-19.5 mm ESL, in which the pectoral rays were still developing, 2 specimens differed by two rays (1.3%) between sides, 63 differed by one ray (40.9%), and 80 *Xiphias* (57.8%) had the same count on both pectoral fins. Of 20 specimens 19.6-668 mm ESL, which had adult counts, 10 differed by one ray between sides and 10 had the same count on both sides.

The position of the pectoral fin in *Xiphias* is on the side of larvae but changes during growth to ventrad in adults near the spot where the pelvic fin is located in most Perciformes. *Xiphias* lacks a pelvic fin and no vestiges of it were found during development (Gregory and Conrad 1937; Leim and Scott 1966; Ovchinnikov 1970; Yasuda et al. 1978).

PECTORAL FIN SUPPORTS

The pectoral rays were directly and indirectly supported by the bones of the pectoral girdle and its suspensorium. In fully developed juveniles the girdle consisted on each side of a scapula and a distal scapular radial (which supported the dorsalmost ray directly and which orginated from scapular cartilage), four large radials (which supported the remainder of the rays directly), a coracoid, and a cleithrum (Figs. 3-5). The scapula was connected to the coracoid by cartilage (Figs. 4, 5). The pectoral suspensorium consisted of a posttemporal, a supracleithrum, and a single postcleithrum. The posttemporal and supracleithrum were connected from the rear of the skull to the lateral side of the posterior process of the cleithrum. The single postcleithrum extended over the abdominal area and articulated on the medial side of the posterior process of the cleithrum (Figs. 3-5). The pectoral

TABLE 2.—Development of left pectoral fin rays for *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). $\bar{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number of rays																		$\bar{X}$	SD
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
3.6-4.5	7																				—	—
4.6-5.5	20	5	6	8	3	2	1	1													1.6	2.03
5.6-6.5			1	3	2	5	2	6	5	5	1										6.4	2.19
6.6-7.5								1	5	3	4	1									8.9	1.12
7.6-8.5									1	2	6	6	5	1							10.7	1.37
8.6-9.5										1	2	3	5	2							11.3	1.08
9.6-10.5												1	6	1	2	1					12.6	1.33
10.6-11.5													3	3	2	1					13.1	1.20
11.6-12.5														1	6	2					14.1	0.60
12.6-13.5														1	2	—	—	1			14.5	1.80
13.6-14.5															2	2	1				14.8	0.89
14.6-15.5													1	—	—	2	2				14.8	1.57
15.6-16.5																	3	2			16.4	0.45
16.6-17.5																	1				—	—
17.6-18.5																1	1	1	1		16.5	1.20
18.6-19.5															1	—	—	1	1		16.3	2.08
19.6-668																	1	10	6	3	17.6	0.89

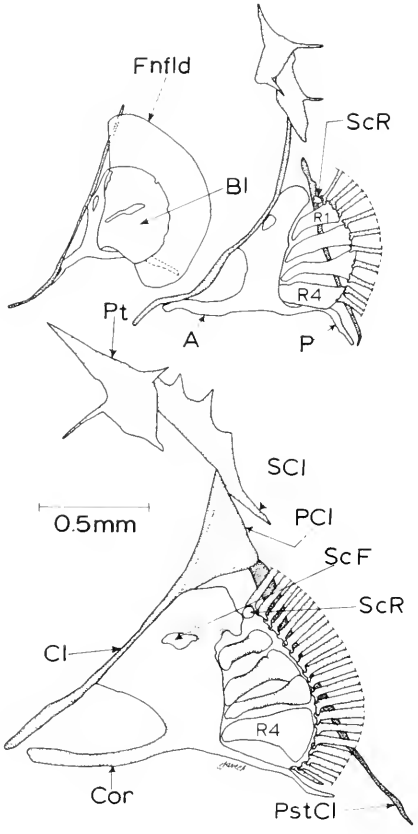
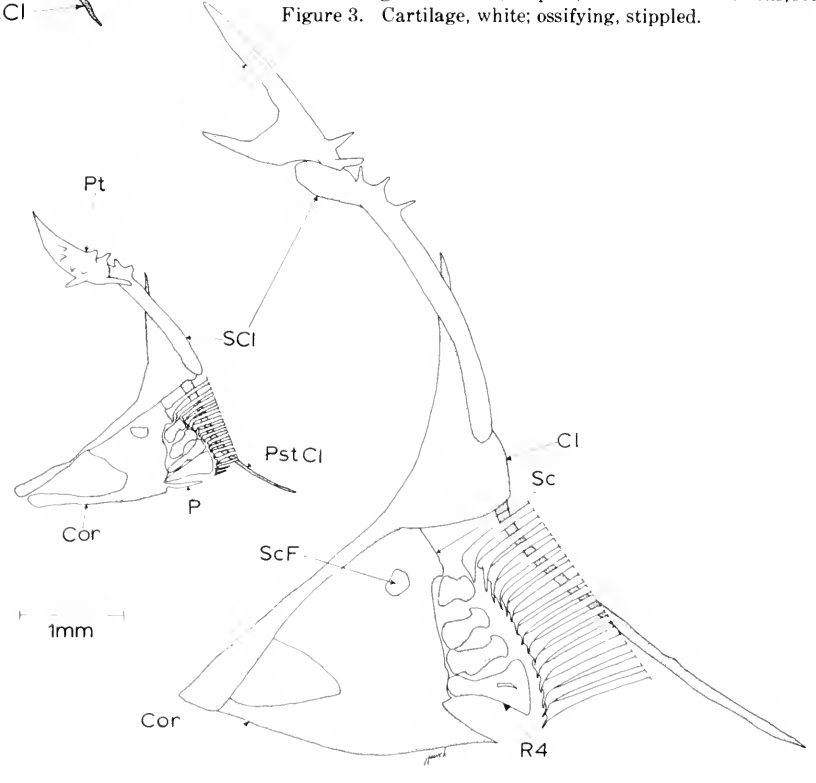


FIGURE 3.—Left lateral external view of the pectoral girdle and suspensorium from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.1 ENL; 7.6 ESL; bottom, 21.4 ESL. A, anterior process of the coraco-scapular cartilage; Bl, larval pectoral fin blade; Cl, cleithrum; Cor, coracoid; Fnfld, larval finfold; P, posterior process of the coraco-scapular cartilage; PCl, posterior process of cleithrum; PstCl, postcleithrum; Pt, posttemporal; R, radial orignating from larval fin blade; ScF, scapular foramen; SCl, supracleithrum; ScR, cartilaginous distal radial originating from scapular cartilage. Cartilage, white; ossifying, stippled.

FIGURE 4.—Left lateral external view of the pectoral girdle and suspensorium from *Xiphias gladius*, showing the ontogeny. The specimens' lengths in millimeters ESL are: left, 33.0; right, 64.6. Sc, scapula; for other abbreviations, see Figure 3. Cartilage, white; ossifying, stippled.



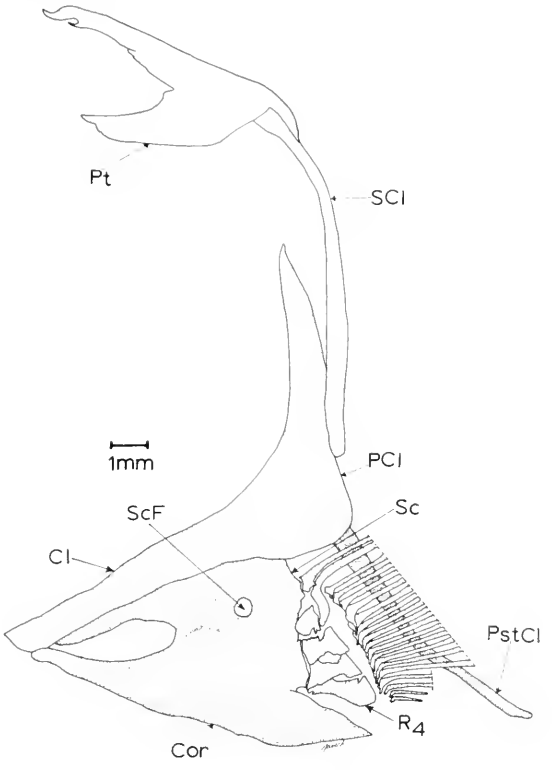


FIGURE 5.—Left lateral external view of the pectoral girdle and suspensorium from a 187 mm ESL *Xiphias gladius*. For abbreviations, see Figures 3 and 4. Cartilage, white; ossifying, stippled.

girdle is only briefly mentioned in Gregory and Conrad (1937) and no detailed description is given.

Our smallest 3.7 mm ENL specimen already had rudiments of a pectoral girdle, consisting of a rod-shaped bony cleithrum, an inverted Y-shaped coraco-scapular cartilage without scapular foramen, and a larval fin blade (similar to the 5.1 mm ENL specimen in Fig. 3) (Table 3). The cleithrum later developed a shelflike dorsal posterior process (Figs. 3-5). The coraco-scapular cartilage at first had long dorsal and long posterior processes and a short anterior process. It developed a foramen on the dorsal process, and the anterior process grew relatively larger and ossified into part of the coracoid, while the posterior process atrophied. Ossification of the scapula started around the scapular foramen and spread over the dorsal process forming the scapula (Figs. 3, 4; Table 3). The larval fin consisted of two parts: a flat cartilaginous semicircular blade surrounded on the circumference by a finfold containing larval actinopterygia (Fig. 3). The semicircular cartilaginous pectoral fin blade developed into the four large radials by first forming elongate holes in the blade. These holes then gradually enlarged to the border of the semicircular cartilage blade, forming separate cartilaginous radials, which later ossified (Figs. 3-5; Table 3).

TABLE 3.—Development of the pectoral girdle and suspensorium for 190 *Xiphias gladius* (3.7 mm ENL-64.6 mm ESL). Length ranges (mm, ENL or ESL) are from "first observance" to "first observance in all specimens."

Part	Appearance in cartilage	Ossification
Posttemporal	—	5.3
Supracleithrum	—	5.3
Postcleithrum	—	5.3
Cleithrum	—	<3.7
Posterior process of cleithrum	—	6.2-6.9
Coraco-scapular cartilage	<3.7	—
Scapular foramen	4.6-5.1	—
Scapula	—	6.6-8.1
Coracoid	—	5.4-6.5
Scapular radial	5.5-9.3	10.6-15.0
Radial No. 1	5.2-5.6	8.8
Radial No. 2	5.2-5.9	9.0-10.0
Radial No. 3	5.4-9.1	9.1-12.0
Radial No. 4	6.8-9.1	13.3-14.7

The pectoral suspensorium, consisting of the posttemporal, supracleithrum, and postcleithrum, was of dermal origin (did not form from cartilage) and was first seen ossifying at 5.3 mm ENL (Table 3). The posttemporal was at first a flat rectangular bone with spines. The spines were lost and a dorsal and ventral process developed, giving the posttemporal the characteristic inverted C shape (Figs. 3-5; Table 3). The supracleithrum was short at first and had spines. It also lost its spines and developed a long posterior process which articulated laterally with the posterior process of the cleithrum (Figs. 3-5; Table 3). Lengthening of the supracleithrum accommodates the migration of the pectoral fin from a lateral position in the larvae to a more ventral position in the adults (Ovchinnikov 1970). The postcleithrum was an elongate rod-shaped bone without spines from the start and articulated medially with the posterior process of the cleithrum (Figs. 3-5; Table 3).

DORSAL FIN

Dorsal fin rays first appeared almost at the same sizes as the anal and caudal rays (Tables 1, 4). The dorsal fin rays developed in the dorsal finfold first at the middle of the body above the 10th-14th myomere in specimens 5.5-6.1 mm ENL. With growth, addition of dorsal fin rays

TABLE 4.—Summary of dorsal fin ray development for 208 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL).

Length, mm ENL or ESL	N	Range, number of dorsal fin rays	Mean, number dorsal fin rays	SD
3.6-4.5	7	0	0	—
4.6-5.5	47	0-32	1.3	6.17
5.6-6.5	31	0-38	23.0	13.92
6.6-7.5	14	27-42	35.7	4.49
7.6-8.5	21	36-45	41.0	2.75
8.6-9.5	13	40-44	42.2	1.44
9.6-10.5	11	40-45	42.2	1.66
10.6-11.5	8	42-47	43.8	1.70
11.6-12.5	9	40-48	44.9	2.40
12.6-13.5	4	42-46	43.8	1.80
13.6-14.5	5	43-48	44.8	2.01
14.6-668.0	38	44-49	46.4	1.23

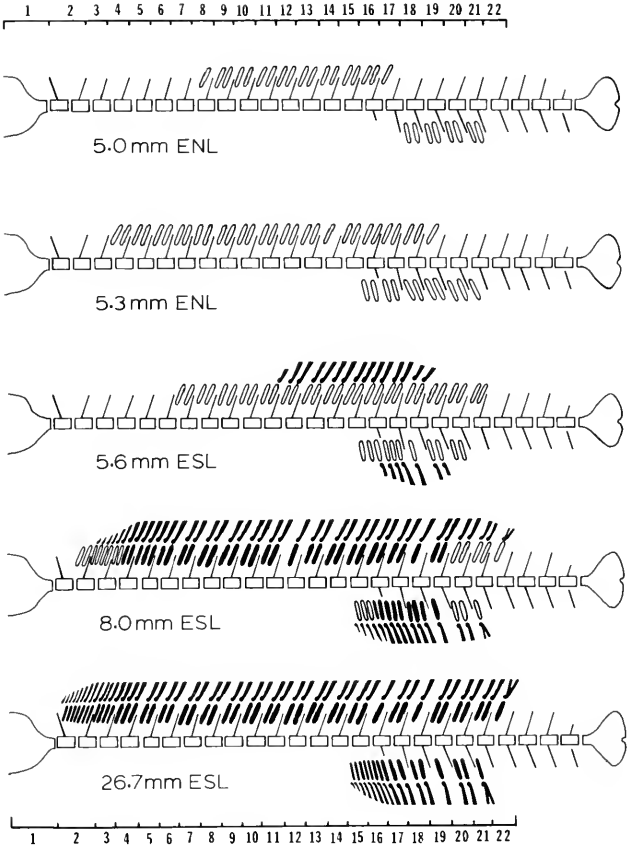


FIGURE 6.—Schematic representation of dorsal and anal fin and pterygiophore development in *Xiphias gladius* in relation to the vertebral column and head. Pterygiophores are represented white when cartilaginous and black when ossifying. Scales represent interneural and interhaemal space numbers and points on scales align with tips of neural and haemal spines.

was in an anterior and posterior direction. The posterior part of the dorsal fin was complete at a smaller size before the anterior part. Adult dorsal fin counts of 44-49 rays (14.6-668 mm ESL, $N = 38$, $\overline{X} = 46.4$, SD = 1.23) were first observed at 8.1 mm ESL, and all specimens longer than 13.8 mm ESL had the adult count (Fig. 6; Table 4). Our counts are in agreement with Arata (1954). Some of Arata's specimens, however, did not have adult counts. The sequence of dorsal fin ray development is similar in *Xiphias* to that of *Coryphaena* reported by Potthoff (1980).

DORSAL FIN PTERYGIOPHORES

In juvenile and adult specimens of *Xiphias* 14.1-668 mm ESL, the pterygiophores consisted of a jointed proximal and distal radial supporting a fin ray. The distal radial was located between the bifurcate base of the fin ray. Each proximal and distal radial and fin ray were forming a series, hence a serial association. Each fin ray also closely approximated the following posterior pterygiophore in a secondary association. Distal radials were present for all fin rays in 14 out of 37 juvenile specimens. Of the remaining 23 specimens 19 had one anteriormost ray and 4 had two anteriormost rays without distal radials (Table 5). Exceptions to the serial and secondary fin ray associations were found at the beginning and end of the fins. The anteriormost pterygiophore supported from one to three rays, most often two (Fig. 7). This pterygiophore consisted of one piece of cartilage, or of a Y-shaped piece, or of two fused pieces (Figs. 7, 8). In 1 of 38 speci-

TABLE 5.—Percent and number of anterior dorsal and anal fin rays without distal radials for 37 *Xiphias gladius* (14.7-668 mm ESL). Percent and number under 0 are specimens in which all fin rays had distal radials.

Item	Number of anterior dorsal and anal fin rays		
	0	1	2
Percent without dorsal distal radial(*N*)	37.8(14)	51.4(19)	10.8(4)
Percent without anal distal radial(*N*)	86.5(32)	13.5(5)	100.0(37)

Anteriormost dorsal pterygiophore shape	Number, dorsal fin rays associated with anteriormost pterygiophore		
	1	2	3
	4	23	2
			6
			2
Anteriormost anal pterygiophore shape	**Number, anal fin rays associated with anteriormost pterygiophore**		
	1	2	3
	1	21	
		10	4
	1		

FIGURE 7.—Threee possible shapes of anteriormost dorsal and anal pterygiophores for 37 *Xiphias gladius* 14.7-668 mm ESL and the number of fin rays associated with each pterygiophore shape.

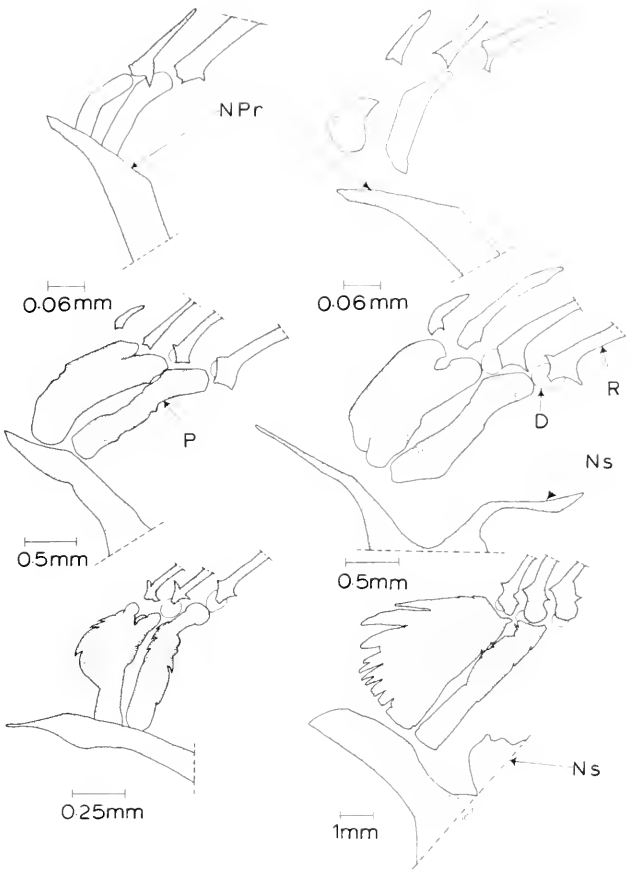


FIGURE 8.—Left lateral view of the two anteriormost dorsal fin pterygiophores with their associated rays in the second interneural space for various sizes of *Xiphias gladius*. Starting from left the specimens' lengths in millimeters ESL are: top row, 15.9, 20.4; middle row, 26.7, 33.6; bottom row, 52.4, 225. D, distal radial; NPr, neural prezygapophysis; Ns, neural spine; P, proximal radial; R, fin ray. Cartilage, white; ossifying, stippled.

mens, no rays were associated with the anterior most pterygiophore. The posteriormost dorsal fin ray was double and was serially associated with the posteriormost pterygiophore (Figs. 9, 10). The double ray lacked a secondary association, but a stay was present under the double ray (Figs. 9, 10). Middle radials were absent in *Xiphias*. Total dorsal pterygiophore count was either equal to or one to two less than the dorsal fin ray count, depending on the number of rays associated with the anteriormost pterygiophore.

In larvae, juveniles, and small adults of *Xiphias* the dorsal proximal radials inserted in the interneural spaces. In 39 juveniles and small adults with fully formed fins, the first interneural space (bounded by head and first neural spine) lacked inserting pterygiophores or predorsal bones. The second interneural space (bounded by first and second neural spines) had four to seven ($\overline{X} = 5.2$), the third space had three to five ($\overline{X} = 4.2$), the fourth space had two to three ($\overline{X} = 2.9$), the fifth space had two to three ($\overline{X} = 2.4$), and the remainder of the interneural spaces had one to three pterygiophores, but usually two (Fig. 11). Usually the posteriormost dorsal pterygiophore inserted in the 22d interneural space and occasionally in the 21st (Fig. 11; Tables 6, 7).

In *Xiphias*, dorsal fin pterygiophores first appeared in cartilage before the fin rays at 4.8 mm ENL, but not until 6.0 mm ENL did all specimens have cartilaginous pterygiophores. Two *Xiphias*, 5.1 and 5.6 mm ENL, lacked dorsal pterygiophores but had some cartilaginous anal pterygiophores. Dorsal pterygiophores were first seen at the center of the body between the 11th and 18th interneural spaces (Fig. 6;

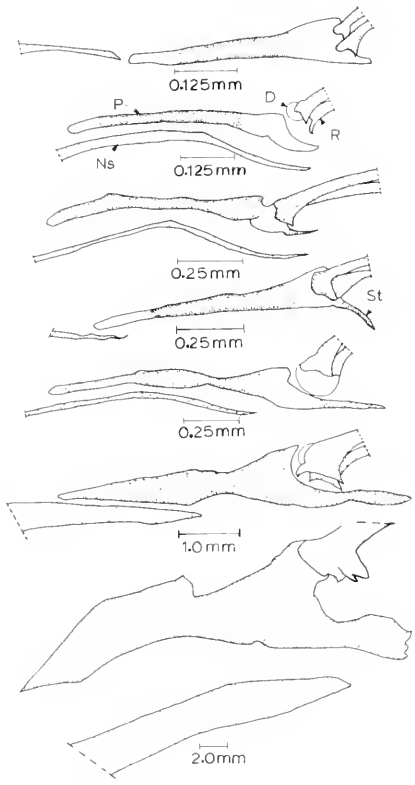


FIGURE 9.—Left lateral view of the posteriormost dorsal pterygiophore from *Xiphias gladius*, showing the ontogeny. Starting from the top and going to the bottom the specimens' lengths in millimeters ESL are: 15.9, 20.4, 26.7, 33.6, 52.4, 225, length unknown for last on bottom, weight 61 lb. St, stay; for other abbreviations, see Figure 8. Cartilage, white; ossifying, stippled.

TABLE 6.—Adult and juvenile position of posteriormost dorsal and anal fin pterygiophores in their interneural and interhaemal spaces for 116 *Xiphias gladius* (7.1-668 mm ESL).

	Interneural space numbers / Interhaemal space numbers			
Item	21 / 20	21 / 21	22 / 21	22 / 22
Number of specimens	29	7	79	1
Percent of specimens	25.0	6.0	68.1	0.9

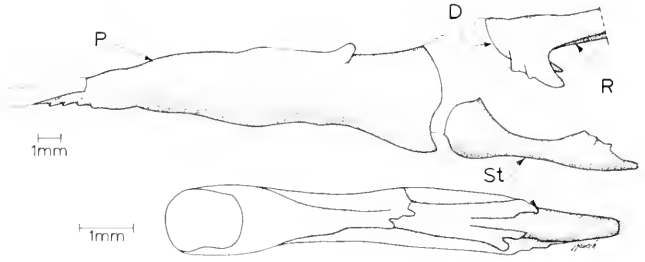


FIGURE 10.—Posteriormost dorsal pterygiophore and its stay from a 668 mm ESL *Xiphias gladius*. Top, left lateral view of proximal and distal radial, double ray and stay; bottom, dorsal view of stay, enlarged. For abbreviations, see Figures 8 and 9. Cartilage, white; bone, stippled.

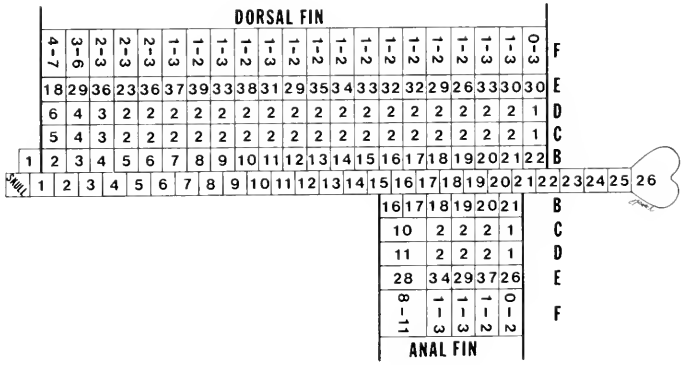


FIGURE 11.—Schematic presentation of common arrangement of pterygiophores and fin rays in relation to neural and haemal spines and vertebrae in 39 *Xiphias gladius* (14.7-668 mm ESL). Method of presentation modified after Matsui (1967). A, skull and vertebrae numbers; B, interneural and interhaemal space numbers; C, number of pterygiophores with highest frequency of occurrence found in the respective ("B") interneural or interhaemal space; D, number of fin rays associated with pterygiophores for indicated interneural or interhaemal space; E, highest frequency of occurrence in 39 *Xiphias* for the number of pterygiophores indicated in "C"; F, range of number of pterygiophores found in the respective ("B") interneural and interhaemal spaces.

Table 7). Addition of cartilaginous pterygiophores was in both anterior and posterior directions. The posteriormost interneural space number 21 or 22 was filled first (Fig. 6; Table 7). Addition of pterygiophores was then in an anterior direction until the anterior interneural space number 2 was occupied (Fig. 6; Table 7). Fin rays followed pterygiophore appearance at the center of the body. Addition of rays followed addition of pterygiophores, with some cartilaginous pterygiophores present anterior and posterior to the developing rays (Fig. 6).

Ossification of dorsal pterygiophores first started at 6.1 mm ENL in the same area and proceeded in the same direction as the cartilage development. Every specimen >8.0 mm ESL had some ossifying pterygiophores, and between 18.2 and 26.7 mm ESL all pterygiophores were ossifying. The last pterygiophore to ossify was the anteriormost in the second interneural space.

TABLE 7.—Development of dorsal and anal fin pterygiophores in the interneural and interhaemal spaces for 205 *Xiphias gladius*. $\bar{X}$ = mean.

Length, mm ENL or ESL	With pterygiophores				With ossifying pterygiophores			
	Anteriormost space no. ($\bar{X}$)		Posteriormost space no. ($\bar{X}$)		Anteriormost space no. ($\bar{X}$)		Posteriormost space no. ($\bar{X}$)	
	Interneural	Interhaemal	Interneural	Interhaemal	Interneural	Interhaemal	Interneural	Interhaemal
3.6-4.5	([1])	([1])	([1])	([1])	([2])	([2])	([2])	([2])
4.6-5.5	[1]3-11(5.0)	[1]16-18(17.1)	[1]17-22(20.0)	[1]19-21(20.1)	([2])	([2])	([2])	([2])
5.6-6.5	[1]2-6 (3.2)	16-18(16.5)	[1]20-22(21.4)	20-22(20.6)	[2]7-9 (8.0)	[2]16-17(16.8)	[2]16-18(17.0)	[2]17-19(18.0)
6.6-7.5	2-4 (2.8)	16-17(16.4)	21-22(21.6)	20-21(20.5)	[2]4-14(9.2)	[2]16-17(16.5)	[2]14-19(17.3)	[2]17-20(18.9)
7.6-8.5	2-3 (2.1)	16-17(16.5)	21-22(21.9)	20-21(20.9)	[2]3-11(5.4)	[2]16-18(16.4)	[2]13-22(19.1)	[2]17-21(19.0)
8.6-9.5	2-3 (2.1)	16-17(16.2)	21-22(21.8)	20-21(21.1)	3-12(4.7)	16-17(16.2)	14-22(19.4)	16-21(19.2)
9.6-10.5	2-3 (2.1)	16-17(16.3)	21-22(21.7)	20-21(20.6)	2-5 (3.5)	16-17(16.3)	19-22(20.5)	19-21(19.8)
10.6-11.5	2	16-17(16.4)	21-22(21.9)	20-21(20.9)	2-5 (3.8)	16-17(16.2)	18-22(20.7)	19-21(20.2)
11.6-12.5	2	16-17(16.4)	21-22(21.7)	20-21(20.6)	2-4 (2.8)	16-17(16.4)	18-22(20.8)	19-21(20.4)
12.6-13.5	2	16-17(16.8)	21-22(21.5)	20-21(20.8)	2-3 (2.5)	16-17(16.8)	21-22(21.3)	19-21(20.0)
13.6-14.5	2	16-17(16.4)	21-22(21.4)	20-21(20.6)	2-3 (2.2)	16-17(16.4)	20-22(21.0)	20-21(20.4)
14.6-15.5	2	16-17(16.6)	21-22(21.8)	20-21(20.8)	2	16-17(16.8)	21-22(21.8)	20-21(20.8)
15.6-16.5	2	16-17(16.2)	21-22(21.4)	20-21(20.4)	2-3 (2.4)	16	21-22(21.4)	20-21(20.4)
16.6-668	2	16-17(16.4)	21-22(21.5)	20-22(20.7)	2	16-17(16.4)	21-22(21.5)	19-21(20.6)

[1]No pterygiophores developed in all or some specimens; these were not used for calculation of means.
[2]No pterygiophores ossified in all or some specimens; these were not used for calculation of means.

Pterygiophores under the middle of the dorsal fin completed development first. Proximal and distal radials first appeared as one piece of cartilage. Then the distal radial cartilage separated from the proximal radial. Ossification of the proximal radial cartilage started at the middle and spread outwards proximally and distally toward the ends. The ends remained cartilaginous in adults, and small sagittal keels developed ventrad during ossification (Fig. 12). Extensive lateral keels were observed on the pterygiophores in the largest 668 mm ESL specimen.

The posteriormost pterygiophores ossified later, but in the same sequence as those in the middle area. The last pterygiophores supported a double ray in series and a stay was present (Figs. 9, 10). The posteriormost pterygiophore and the stay ossified from the same piece of cartilage (Figs. 9, 10).

The anteriormost pterygiophores were the last to ossify. The first anteriormost pterygiophore developed a large anterior sagittal keel (Fig. 8).

Distal radials developed from a piece of cartilage that separated during development from the distal portion of the cartilaginous pterygiophores and was situated between the bifurcate bases of the serial fin rays (Figs. 8, 12, 13). Ossification of all distal radials occurred after cartilage separation. At first the left and right sides of the distal radial cartilage ossified to form two pieces of bone. Ossification continued until the two bones were joined (Figs. 14, 15). All dorsal fin rays associated with the distal radials had bifurcated bases (Figs. 14, 15).

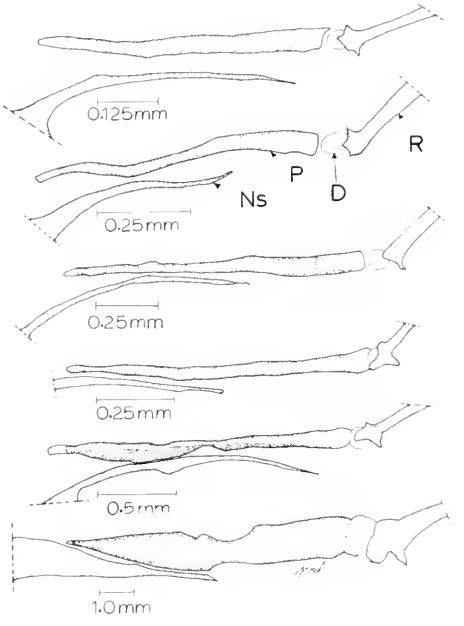


FIGURE 12.—Left lateral view of a dorsal pterygiophore from the 11th interneural space of *Xiphias gladius*, showing the ontogeny. Starting from the top and going to the bottom the specimens' lengths in millimeters ESL are: 15.9, 20.4, 26.7, 33.6, 52.4, 225. For abbreviations, see Figure 8. Cartilage, white; ossifying, stippled.

ANAL FIN

Anal fin rays first appeared at about the same sizes as the dorsal and caudal rays (Tables 1, 8). The anal rays developed in the anal finfold first at the middle of the fin below myomeres 18-20 in specimens 5.3-6.1 mm ENL. Anal rays were

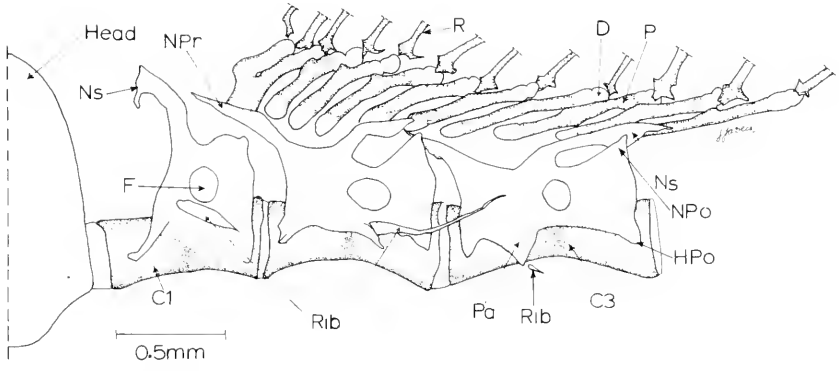


FIGURE 13.—Anteriormost three vertebrae and pterygiophores with fin rays from a 35.9 mm ESL *Xiphias gladius*. C, centrum; D, distal radial; F, neural foramen; HPo, haemal postzygapophysis; NPo, neural postzygapophysis; NPr, neural prezygapophysis; Ns, neural spine; P, proximal radial; Pa, parapophysis; R, ray.

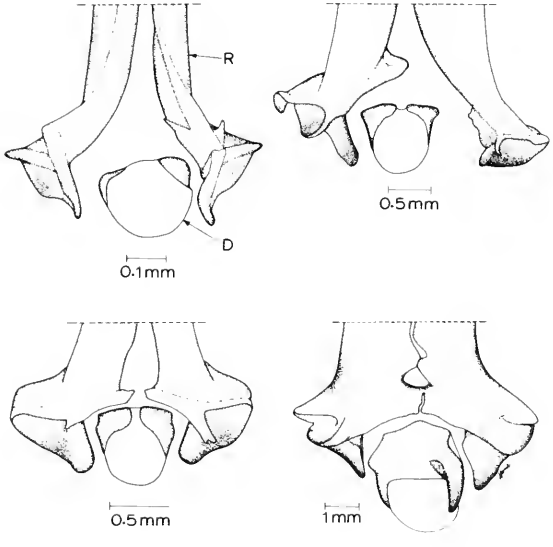


FIGURE 14.—Anterior view of the 12th dorsal ray and its distal radial from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters ESL are: top, 64.6, 187; bottom, 225, 668. D, distal radial; R, fin ray. Cartilage, white; ossifying, stippled.

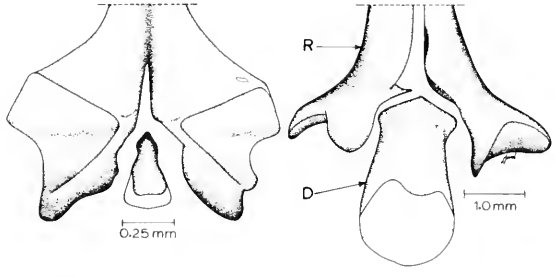


FIGURE 15.—Anterior view of two fin rays and their distal radials from juvenile *Xiphias gladius*. The specimens' lengths in millimeters ESL are: left, 225, first anteriormost dorsal ray; right, 668, next to last posteriormost dorsal ray. D, distal radial; R, fin ray. Cartilage, white; bone, stippled.

added in an anterior and posterior direction (Fig. 6). Adult anal counts of 16-19 rays (10.6-668 mm ESL, $N = 66$, $\bar{X} = 17.1$, SD = 0.81) were first observed at 7.8 mm ESL and all specimens longer than 10.6 mm ESL had the adult counts (Fig. 6; Table 8). Our counts generally agree with those of Arata (1954), except we had two specimens with 19 anal rays; Arata had none.

TABLE 8.—Development of anal fin rays for 213 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). $\bar{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number of anal fin rays																		
	0	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	$\bar{X}$	SD
3.6-4.5	7																	—	—
4.6-5.5	43	2	—	—	—	—	1	—	1									0.6	2.06
5.6-6.5	6	—	—	2	—	1	3	—	8	2	4	2	4	1				9.5	5.17
6.6-7.5									1	—	5	1	4	2	1			14.2	1.50
7.6-8.5												1	8	5	5	2		16.0	0.92
8.6-9.5													2	8	3			16.1	0.72
9.6-10.5													1	6	3	1	1	16.6	1.04
10.6-668														13	37	15	1	17.1	0.81

ANAL FIN PTERYGIOPHORES

The description of the dorsal fin pterygiophores in the previous section may be applied to anal fin pterygiophores because of the similarities between the two. Anal pterygiophores were inserted in the interhaemal spaces. These spaces were numbered the same as the opposing interneural spaces. Anteriormost (first) interhaemal space number 16 or 17 was bound anteriorly by the stomach, intestine, and anus and posteriorly by the first haemal spine. The first haemal spine was positioned on the 16th or 17th centrum. If it occurred on the 16th centrum, it was of variable length and often did not reach the pterygiophores. If the first haemal spine was on the 17th centrum, it always reached past the pterygiophores. The count for the 16th and 17th interhaemal space was summed because we were not always able to determine a division between the two spaces (Fig. 11).

Total number of anal pterygiophores in 31 of 37 specimens with full counts was one less than the anal fin ray count. In 2 of 37 specimens, it was the same and in 4 of 37 it was two less. The anteriormost anal pterygiophore supported from one to three rays, most often two (Fig. 7). This pterygiophore consisted of one piece of cartilage, normal in shape (Fig. 16), or of a vestige (Fig. 7). The vestigial piece may fuse to the next posterior pterygiophore to form an inverted Y shape (Fig. 16), or the inverted Y shape may originate from one piece of cartilage (Figs. 7, 16). An anterior sagittal keel developed on the anteriormost anal pterygiophore (Fig. 16), but this keel was not as large as on the first dorsal pterygiophore (Fig. 8).

The posteriormost anal pterygiophore had the same structure as its dorsal counterpart and inserted most often into the 20th or 21st interhaemal space, which was usually one space anterior to the posteriormost dorsal insertion (Fig. 11; Table 6).

In juveniles and small adults of *Xiphias* with fully formed fins the anteriormost interhaemal spaces 16 and 17 had 8-11 ($\overline{X}$ = 9.9, N = 40) pterygiophores. The remaining three or four interhaemal spaces had one to two or one to three pterygiophores each (Fig. 11). The posteriormost 21st interhaemal space had none or one to two pterygiophores. Only 1 specimen out of 116 had a pterygiophore in the 22d interhaemal space (Table 6).

Development and structure of the anal fin

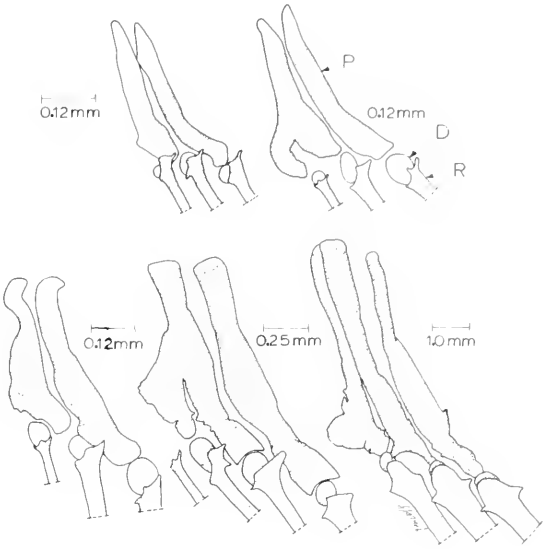


FIGURE 16.—Left lateral view of two or three anteriormost anal fin pterygiophores from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters ESL are: top row, 15.9, 20.4; bottom row, 33.0, 64.6, 225. D, distal radial; P, proximal radial; R, fin ray. Cartilage, white; ossifying, stippled.

pterygiophores was the same as in the dorsal supports. Cartilaginous anal pterygiophores first appeared before anal fin rays and most of the time concurrently with dorsal pterygiophores below myomeres 18-20 (which approximately corresponds to interhaemal spaces 18-20) (Fig. 6; Table 7). Addition of cartilaginous pterygiophores was in an anterior and posterior direction. The posteriormost interhaemal spaces 20 or 21 were filled first. Last to develop was the anteriormost anal pterygiophore (Fig. 6). Fin rays followed pterygiophore appearance as in the dorsal fin (Fig. 6).

Ossification of anal fin pterygiophores first started between 6.0 and 8.0 mm ENL or ESL in the same area of first appearance in cartilage and proceeded in the same directions as cartilage development (Fig. 6; Table 7). All anal pterygiophores were ossifying between 12.0 and 25.1 mm ESL.

Development and ossification of individual anal pterygiophores is similar to the dorsal pterygiophores (Fig. 16). The posteriormost anal pterygiophore develops a stay and supports a double ray serially as does its dorsal counterpart.

Distal radials developed in the anal fin as in the dorsal fin (Fig. 14). Almost all rays had a distal radial between their bifurcate base. Only 5 out of

37 specimens did not have a distal radial for the anteriormost ray (Table 5).

CAUDAL FIN

Caudal fin rays first appeared at about the same sizes as the dorsal and anal rays (Table 1). The caudal fin rays developed in the caudal finfold ventrad in preflexion larvae first on hypurals 2 and 3 and were added in an anterior and posterior direction. After complete notochord flexion between 6.3 and 8.0 mm ESL, the secondary caudal rays developed dorsad and ventrad in an anterior direction. Caudal rays were first seen in a 5.4 mm ENL specimen and all larvae longer than 6.1 mm ENL had some caudal rays developing (Table 9). The full complement of 9+8 principal rays developed between 8.8 and 11.0 mm ESL. All *Xiphias* longer than 26.6 mm ESL had the adult count of (8-10)+9+8+(9-11)=34-38 (N = 15, $\bar{X}$ = 35.9, SD = 1.55) rays (Tables 9, 10). The upper and lower caudal lobe had equal numbers of rays or they differed by one ray (Table 10). A procurrent spur (Johnson 1975) was not oberved in *Xiphias*.

TABLE 9.—Caudal fin ray development for 200 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). SCR, secondary caudal rays. PCR, principal caudal rays. $\bar{X}$ = mean, SE = standard error of the mean. Specimens are undergoing notochord flexion between dashed lines at 6.3-8.0 mm ENL.

Length, mm ENL or ESL	Upper		Lower		Total fin ray count			
	SCR	PCR	PCR	SCR	Range	$\bar{X}$	SE	N
3.6-4.5	0	0	0	0	0	—	—	7
4.6-5.5	0	0-3	0-3	0	0-6	0.2	1.36	46
5.6-6.5	0	0-6	0-8	0	0-14	4.9	3.83	30
6.6-7.5	0	2-7	2-8	0	4-15	9.9	2.99	14
7.6-8.5	0	4-8	4-8	0-1	8-17	13.7	2.62	19
8.6-9.5	0-1	5-9	6-8	0-2	11-19	15.5	2.77	12
9.6-10.5	0	7-9	8	0-2	16-20	17.6	1.33	11
10.6-11.5	0-1	7-9	8	0-2	16-20	18.1	1.50	9
11.6-12.5	0-2	9	8	2	19-21	19.6	0.85	8
12.6-13.5	0-3	9	8	1-3	18-23	21.3	2.20	4
13.6-15.5	0-3	9	8	2-3	19-23	21.5	1.41	8
15.6-17.5	3-5	9	8	3-5	23-27	24.3	1.71	6
17.6-26.5	4-7	9	8	4-8	25-32	26.0	1.99	11
26.6-668	8-10	9	8	9-11	34-38	35.9	1.55	15

TABLE 10.—Adult caudal fin ray counts for 15 *Xiphias gladius* (26.7-225, 668 mm ESL). USCR = upper secondary caudal rays, PCR = principal caudal rays, LSCR = lower secondary caudal rays.

Total fin ray count	USCR	+	PCR	+	LSCR	N
34	8	+	17	+	9	4
35	9	+	17	+	9	2
36	9	+	17	+	10	3
37	10	+	17	+	10	3
38	10	+	17	+	11	3

CAUDAL FIN SUPPORTS

The caudal fin rays were supported by some of the bones of the hypural complex and only two posteriormost centra (PU_2 and urostyle) were involved in the support (Fig. 17). The bones which supported the fin rays directly or indirectly in larvae and juveniles of *Xiphias* were two centra (PU_2 and urostyle), one specialized neural arch, three epurals, one paired uroneural, five autogenous hypural bones, one autogenous parhypural, and one autogenous haemal spine. One of 164 specimens examined had the unusual count of 16+11=27 vertebrae and had two autogenous haemal spines on preural centra 2 and 3. We were able to see all these supporting bones during development (Figs. 18-23; Table 11), but in the adults some parts were ontogenetically fused.

Between 3.7 and 6.2 mm ENL, *Xiphias* had a straight notochord in the caudal area. Notochord flexion was between 6.3 and 8.0 mm ENL. Before notochord flexion hypurals 1-4, the parhypural (Ph), and the haemal spine and arch (Hs) of the future preural centrum 2 were developing ventrad in cartilage (Fig. 18; Table 11). Dorsad the neural arch (Ns) of the future preural centrum 3, the specialized neural arch ("Na") of the future preural centrum 2, and the three epurals (Ep) were developing from cartilage (Fig. 19). Appearance of the cartilaginous parts was from anterior to posterior. After notochord flexion a cartilaginous hypural 5 (Hy) and a bony uroneural (Un) developed between 9.8 and 12.5 mm ESL (Figs. 20-21; Table 11).

The parhypural and hypurals 1-5 developed from separate pieces of cartilage. This is shown for the parhypural and hypurals 1-2 in Figure 18. Joining of the proximal portions of the parhypural and hypurals 1-2 by cartilage starts with the parhypural and hypural 1 between 5.4 and 5.6 mm ENL and extends to hypural 2 at 5.7 mm ENL. All specimens have the parhypural and hypurals 1-2 joined proximally with cartilage at 6.9 mm ENL or ESL as shown in Figures 19 and 20. Hypurals 3-5 are never joined by cartilage during development (Figs. 19-21). The cartilaginous proximal joint is lost during development when the hypurals are fully ossified between 27 and 34 mm ESL (Fig. 22).

Ossification of the cartilage bone in the caudal complex of *Xiphias* started with the preural

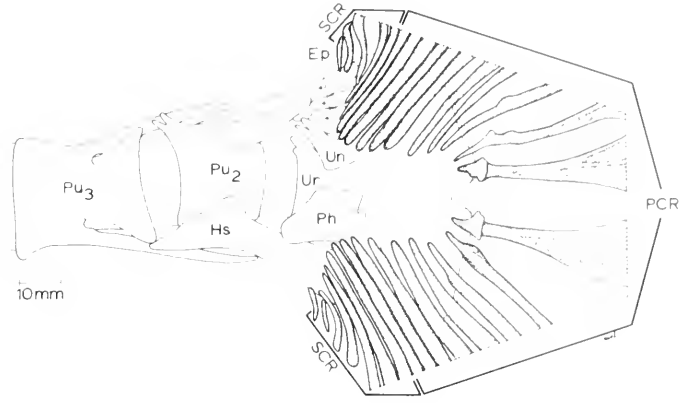


FIGURE 17.—Left lateral view of the adult caudal complex from *Xiphias gladius* of unknown length, 48 lb, showing fin ray articulation in relation to the caudal parts. Ep, epural; Hs, autogenous haemal spine; PCR, principal caudal rays; Ph, parhypural; Pu, preural centrum; SCR, secondary caudal rays; Un, uroneural; Ur, urostyle. Caudal complex bones, white; caudal rays, stippled.

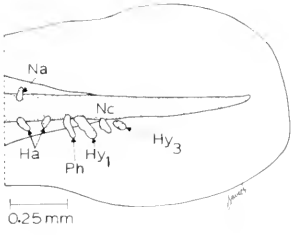


FIGURE 18.—Left lateral view of the caudal complex of a 5.1 mm ENL *Xiphias gladius*. Ha, haemal arch; Hy, hypural; Nc, notochord; Na, neural arch; Ph, parhypural. Cartilage, stippled.

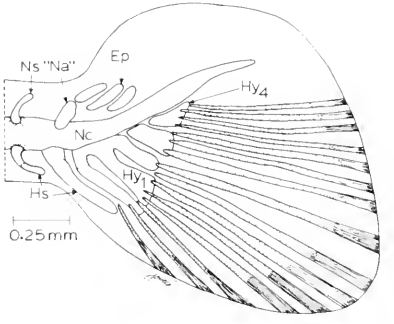


FIGURE 19.—Left lateral view of the caudal complex of a 8.8 mm ESL *Xiphias gladius*. Hs, haemal spine; "Na", specialized neural arch; Ns, neural spine; for other abbreviations, see Figures 17 and 18. Cartilage, white; bone, stippled.

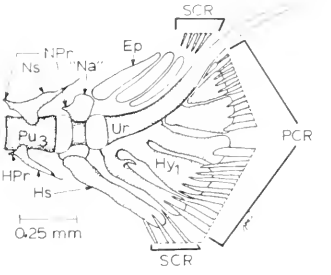


FIGURE 20.—Left lateral view of the caudal complex of a 12.6 mm ESL *Xiphias gladius*. HPr, haemal prezygapophysis; NPr, neural prezygapophysis; for other abbreviations, see Figures 17-19. Cartilage, white; ossifying, stippled.

TABLE 11.—Length ranges at which parts of the caudal complex appear in cartilage and ossify in 173 *Xiphias gladius* (5.4 mm ENL-225 mm ESL). Pu = preural centrum. Brackets denote fusion of separate structures during development.

	Length range (mm, ENL or ESL) of first appearance in cartilage	Length range (mm, ENL or ESL) of first evidence of ossification	First evidence of fusion (mm, ESL)
Pu_2 centrum	—	6 2- 9 0	
Specialized neural arch	5 4-6.5	7.1-12 3	
Epural			
anterior	5.7-6.8	10.3-13.7	
middle	5 4-6.8	10 3-13 7	
posterior	5.4-7.1	16 2-17 6	
Uroneural	—	9 8-12 3	
Hypural 5	9 8-12.5	16.0-17 7	
Hypural 4	5.7-7.9	9 4-13.7	17 2-26.7
Hypural 3	5.3-6.1	7 1-10 7	131 -?
Urostyle	—	6 2-9 1	
Hypural 2	5 1-5 6	7 1-9 7	17 2-22 6
Hypural 1	5.0-5.5	7 1-9 2	
Parhypural	5.0-5.5	7 1-9 2	
Pu_2 haemal spine	5 1-6 1	7 1-10.9	

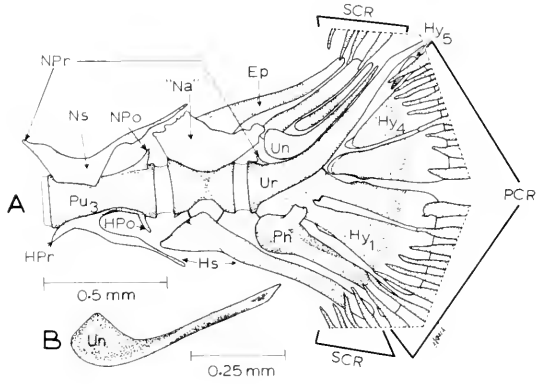


FIGURE 21.—The caudal complex of a 21.4 mm ESL *Xiphias gladius*. A, left lateral view of the complex; B, left lateral view of normal uroneural, enlarged. HPo, haemal postzygapophysis; NPo, neural postzygapophysis; for other abbreviations, see Figures 17-20. Cartilage, white; ossifying, stippled.

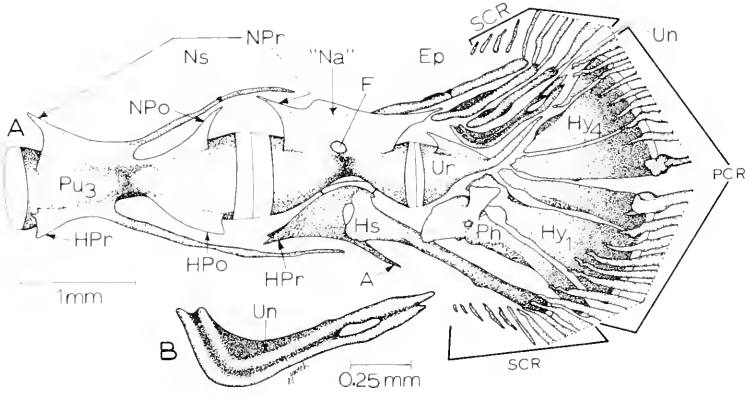


FIGURE 22.—The caudal complex of a 52.4 mm ESL *Xiphias gladius*. A, left lateral view of the complex; B, left lateral view of the anomalous uroneural, enlarged. A, anomalous secondary haemal spine; F, neural foramen; for other abbreviations, see Figures 19-21. Cartilage, white; ossifying, stippled.

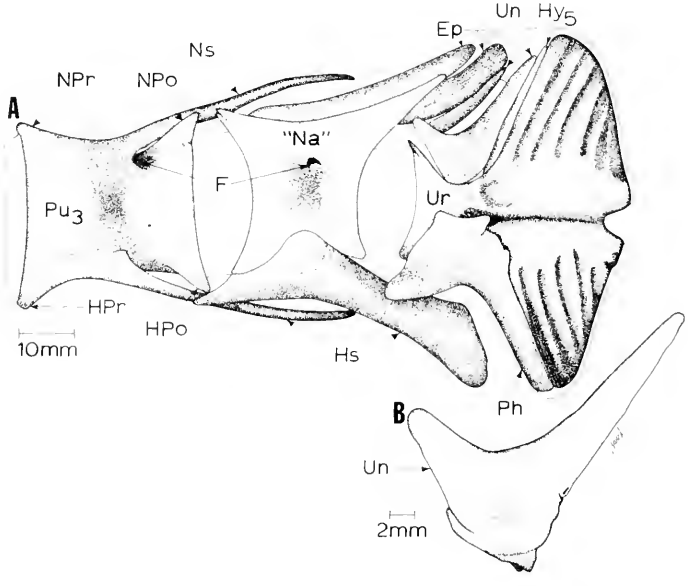


FIGURE 23.—The bones of the caudal complex from an adult *Xiphias gladius* length unknown, 61 lb. A, left lateral view of the caudal bones; B, left lateral view of the normal uroneural, enlarged. For abbreviations, see Figures 19-21. Cartilage, white; bone, stippled.

centrum 2 and the urostyle at 6.2 mm ENL-9.1 mm ESL. Ossification then proceeded from the haemal spine of the preural centrum 2 dorsad to the hypurals. Last to ossify between 16.0 and 17.7 mm ESL was hypural 5 (Table 11). The specialized neural arch of preural centrum 2 began ossification at 7.1-12.3 mm ESL followed by the three epurals. The posteriormost epural was last to ossify between 16.2 and 17.6 mm ESL (Table 11). The paired uroneural was not a cartilage bone and it was first present between 9.8 and 12.3 mm ESL before epural ossification (Table 11). In a few specimens the uroneural had an anomalous shape as if it had fused from two parts (Fig. 22).

During development of the hypural complex, a parhypurapophysis and a hypurapophysis (Lundberg and Baskin 1969; Nursall 1963) were observed on the parhypural and hypural 1. From a dorsal view the parhypural and hypural 1 are bifurcated as shown in Figure 24. This bifurcation can be observed in the adults on the autogenous parhypural but is absent on hypural 1, which then is fused to the hypural plate. A tunnellike foramen develops between the tips and rear of the parhypural prezygapophyses for the haemal canal on the proximal surface of the parhypural. This tunnel was not yet developed in a 44.1 mm ESL specimen (Fig. 24) but was fully formed in our 668 mm ESL specimen.

In adults of *Xiphias*, hypurals 1-4 fuse with each other and the urostyle, forming a single hypural plate with a notch posteriorly at the center. Grooves present on the plate formed because of articulating rays (Gregory and Conrad 1937) (Fig. 23). The epurals, the uroneural, hypural 5, the parhypural, and the haemal spine of preural centrum 2 remained autogenous in the adults. Fusion between hypurals 4 and 3 and 1 and 2 started distad from the articular cartilage in an anterior direction at 17.2-26.7 mm ESL (Figs. 21, 22; Table 11). Fusion of the two hypural plates, however, was in a posterior direction starting proximally. We could not determine the size at which the dorsal and ventral hypural plates fused with each other and with the urostyle because of insufficient samples (Fig. 1; Table 11).

The parhypural and hypurals 1-5 supported the principal caudal rays. Only on one occasion did the haemal spine of preural centrum 2 support a principal caudal ray, but this is not shown in Table 12. The distribution of principal rays on the hypural bones can only be seen in larvae and small juveniles (Figs. 19-22; Table 12).

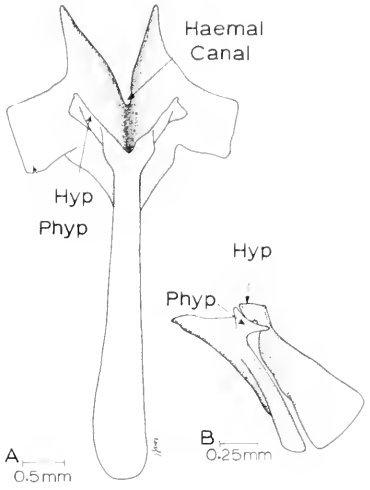


FIGURE 24.—The parhypural and hypural 1 from a 44.1 mm ESL *Xiphias gladius*. A, dorsal view, enlarged; B, left lateral view. Hyp, hypurapophysis; Phyp, parhypurapophysis. Cartilage, white; bone, stippled.

TABLE 12.—Distribution of principal caudal rays on the hypurals in 66 *Xiphias gladius* (8.8-64.6 mm ESL).

Part	Number of principal caudal rays					
	1	2	3	4	5	6
Parhypural	2	61	3			
Hypural 1			1	18	47	
Hypural 2	49	17				
Hypural 3		15	48	3		
Hypural 4			1	18	43	4
Hypural 5	38	28				

VERTEBRAL COLUMN

Of 164 *Xiphias* 5.3 mm ENL-668 mm ESL, 1 (0.6%) had 15+10=25 vertebrae, 95 (57.9%) had 15+11=26, 65 (39.7%) had 16+10=26, and 3 (1.8%) had 16+11=27 (Nakamura et al. 1968; Ovchinnikov 1970).

All centra except the first anteriormost, the urostyle, and preural centrum 2 had neural pre- and postzygapophyses, and neural arches and spines (Figs. 25-27). The first anteriormost centrum lacked a neural prezygapophysis (Figs. 13, 27), preural centrum 2 had a neural prezygapophysis, a specialized (open) neural arch, and a neural postzygapophysis (Figs. 22, 23). The urostyle had only a neural prezygapophysis (Figs. 21-23). All precaudal vertebrae except the anteriormost had parapophyses (Figs. 13, 25,

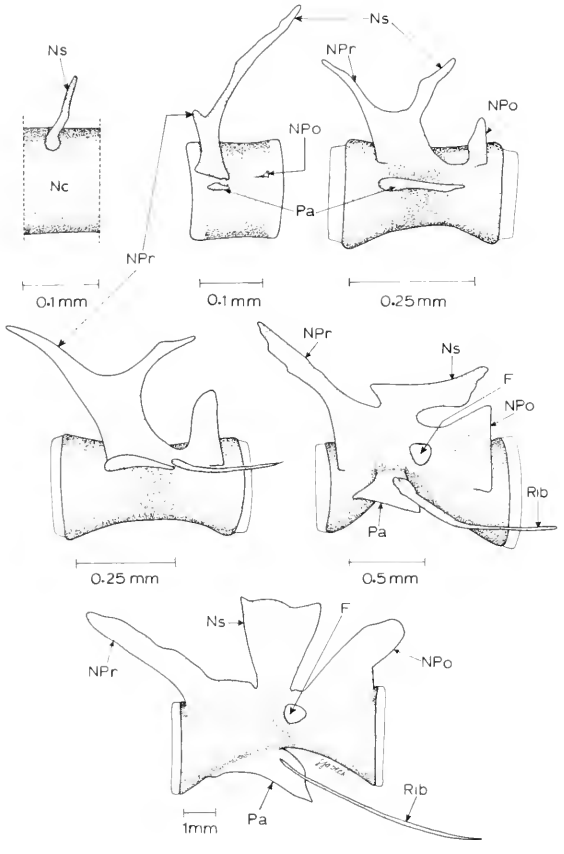


FIGURE 25.—Left lateral view of the second anteriormost vertebra from *Xiphias gladius*, showing the ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.1 ENL, 7.8 ESL,12.6 ESL; center, 21.4 ESL, 52.4 ESL; bottom, 225 ESL. F, neural foramen; Nc, notochord; NPo, neural postzygapophysis; NPr, neural prezygapophysis; Ns, neural spine; Pa, parapophysis. Cartilage, white (except in 5.1 mm ENL specimen in top row left where entire stippling signifies cartilage); ossifying, stippled.

26). Haemal postzygapophyses were present on precaudal vertebrae numbers 3 to 15, sometimes on 2 to 15 (Figs. 13, 26).

All caudal vertebrae had nonautogenous haemal spines, except preural centrum 2 and the urostyle. Preural centrum 2 had an autogenous haemal spine. The urostyle had an autogenous parhypural with a tunnellike foramen for the haemal canal. The parhypural is homologous to the autogenous haemal spine of preural centrum 2 (Figs. 20-24). The 16th centrum sometimes lacked a haemal spine, sometimes had a vestigial haemal spine, or it had a normal haemal spine. Haemal pre- and postzygapophyses were present on all caudal centra except on preural centrum 2 and the urostyle. Neural foramina were present on most precaudal and caudal centra on larger specimens (Figs. 13, 22, 23, 25-28).

Five out of eight *Xiphias* with all ribs developed had six paired ventral ribs, which loosely articulated with the parapophyses on centra 1-4, 14, and 15 (Figs. 25-27). Two specimens had seven pairs of ribs on centra 1-5, 14, and 15 and on centra 1-4 and 13-15. One *Xiphias* had nine pairs on centra 1-6 and 14-16.

The neural arches fuse distally during ossification to form neural spines. The fusion and spine formation is over a size range and proceeds from posterior in an anterior direction (Fig. 27; Table 13). Our largest four specimens of *Xiphias*, 131-668 mm ESL, had three to six anterior neural arches and spines split. These arches and spines remain split in adults (Bruce B. Collette[3]).

Development of the centra starts with the appearance of distally opened cartilaginous neural arches. One arch was seen behind the head on top of the notochord in our smallest 3.7 mm ENL specimen (Fig. 29). As length in *Xiphias* increased, more arches were added in a posterior direction (Fig. 29; Table 14). All specimens >6.5 mm ENL had the complete count of 25 neural arches.

Two cartilaginous split haemal arches were first observed at 5.0 mm ENL when 16 neural arches were present. The two haemal arches were opposite the 16th and future 17th neural arch. Additional haemal arches and spines were added in a posterior direction (Fig. 29; Table 15).

[3]Bruce B. Collette, Systematic Zoologist, National Marine Fisheries Service, NOAA, Systematics Laboratory, Washington, DC 20560, pers. commun. July 1981.

TABLE 13.—Number of split neural arches and spines counted from anterior to posterior for various size ranges in 159 *Xiphias gladius* 5.5 mm ENL-668 mm ESL. N = number of specimens, $\bar{X}$ = mean.

Length, mm ENL or ESL	Centrum number with split neural arches and spines																					N	$\bar{X}$
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24		
5.5-6.9									1	5	2	5	3	3	5	1	1	3	1	1	2	5	38	17.1
7.0-13.3					5	5	12	18	18	10	3	2	1	—	2	—	—	—	—	—	—	1	77	10.7
13.6-64.6				2	6	8	17	6	—	1													40	8.6
131-668	1	—	2	1																			4	4.8

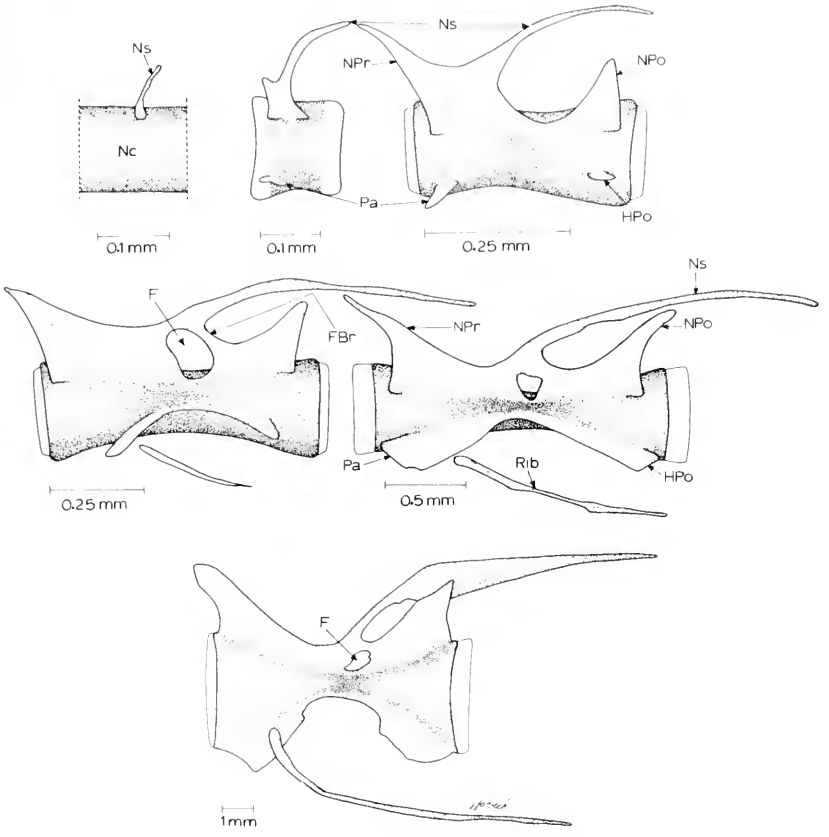


FIGURE 26.—Left lateral view of the 15th vertebra from *Xiphias gladius*, showing the ontogeny. Starting from top left the specimens in millimeters ENL or ESL are as in Figure 25. FBr, foraminal bridge; HPo, haemal postzygapophysis; for other abbreviations, see Figure 25. Cartilage, white (except in 5.1 mm ENL specimen in top row left, where entire stippling signifies cartilage); ossifying, stippled.

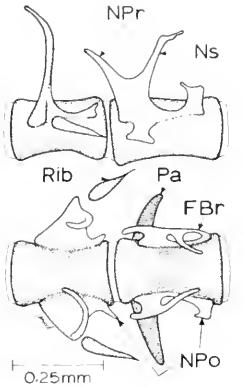


FIGURE 27.—First and second anteriormost vertebrae from a 12.8 mm ESL *Xiphias gladius*. Top, left lateral view; bottom, dorsal view. For abbreviations, see Figures 25 and 26.

All specimens >6.0 mm ENL had the complete count of eight or nine haemal arches and spines.

Ossification of the vertebral column started at 4.4 mm ENL anteriorly at the bases of the neural arches. All specimens longer than 5.0 mm ENL had some anterior vertebral column ossification. The ossification was in a posterior direction as length increased until all centra including the urostyle were ossifying in some specimens between 6.1 mm ENL and 8.1 mm ESL (Fig. 29). In specimens >8.1 mm ESL all entra had some ossification.

The development of the neural and haemal pre- and postzygapophyses is shown in Figures 20-23 and 25-28. Neural prezygapophyses developed on all centra except the anteriormost centrum (Figs. 13, 27) and neural postzygapophyses developed on all centra except the urostyle (Figs. 21-23, 25-28). Haemal prezygapophyses developed on all haemal spines and shifted dorsad and anteriorly onto the centrum during ontogeny (Figs. 20-23, 28); the haemal prezygapophyses on preural centrum 2 and on the parhypural remained on the autogenous haemal spine and the autogenous parhypural (Figs. 21-23).

A neural foramen developed on each centrum except on the urostyle by first developing a neural postzygapophysis (Figs. 25-28). Then an anteriorly directed process developed on the anterodorsal side of the postzygapophysis, which joined the neural spine forming a neural foraminal bridge (Figs. 27, 28).

The neural prezygapophysis of the second anterior centrum developed an entirely different shape than all other prezygapophyses and could be taken for a neural spine on small juvenile or

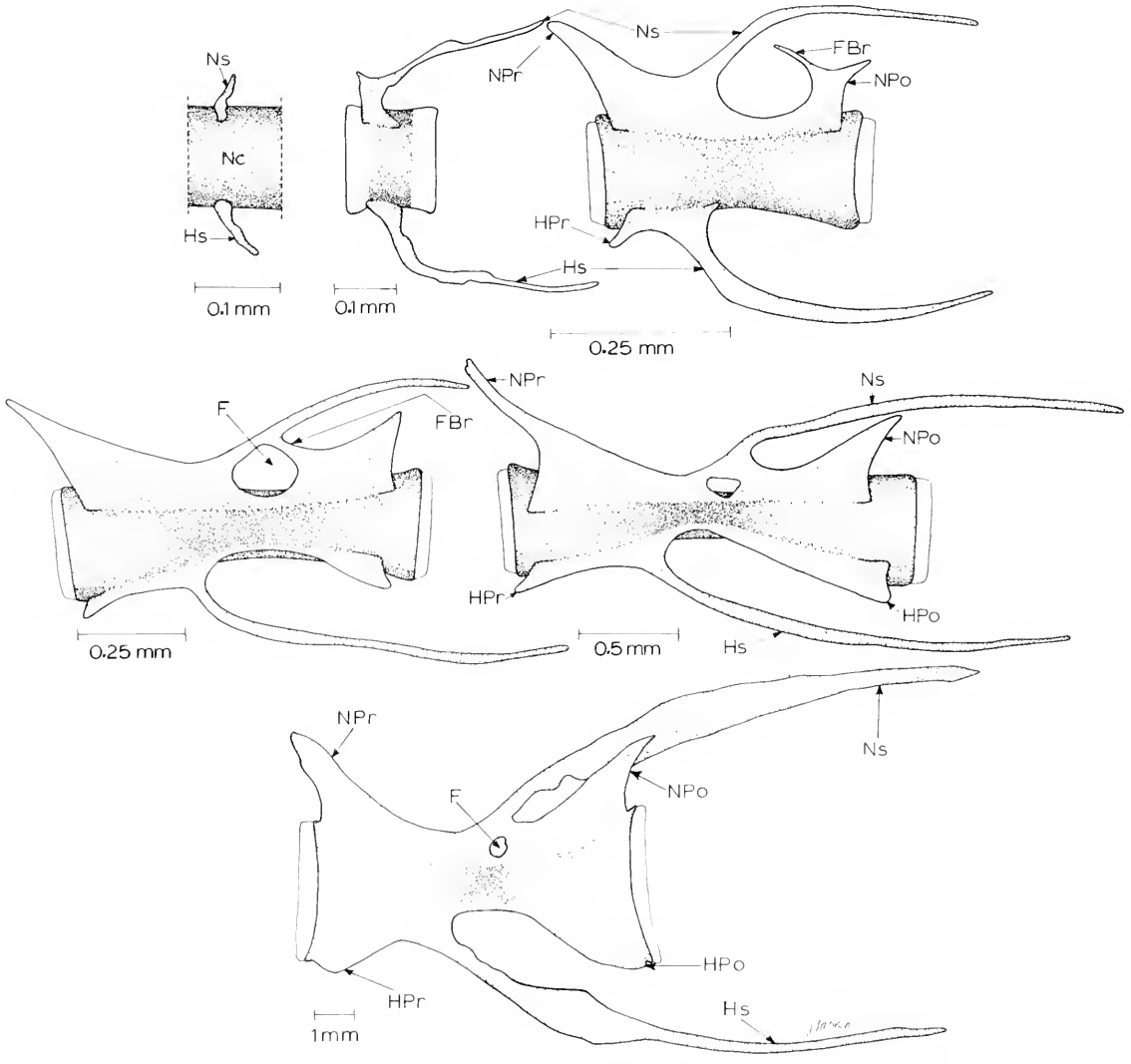


FIGURE 28.—Left lateral view of the 17th vertebra from *Xiphias gladius*, showing the ontogeny. Starting from top left the specimens in millimeters ENL or ESL are as in Figure 25. Hs, haemal spine; HPr, haemal prezygapophysis; for other abbreviations, see Figures 25 and 26. Cartilage, white (except in 5.1 mm ENL specimen in top row left, where entire stippling signifies cartilage); ossifying, stippled.

TABLE 14.—Development of the neural spines on the anterior to posterior numbered centra for 97 *Xiphias gladius* 3.7-7.0 mm ENL or ESL. N = number of specimens, $\bar{X}$ = mean.

Length, mm ENL or ESL	Centra with neural spines																									N	$\bar{X}$
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25		
3.6-4.0	1																									1	—
4.1-4.5	3	1	—	1	—	—	—	1																		6	2.8
4.6-5.0		1	2	8	5	2	—	1	—	—	1	—	—	—	—	1										21	5.3
5.1-5.5				1	1	1	1	1	—	—	2	—	—	1	1	—	—	—	—	—	1	—	6	5	5	26	18.7
5.6-6.0																				1	2	—	3	6	5	17	23.5
6.1-6.5																							3	3	11	17	24.5
6.6-7.0																									9	9	25.0

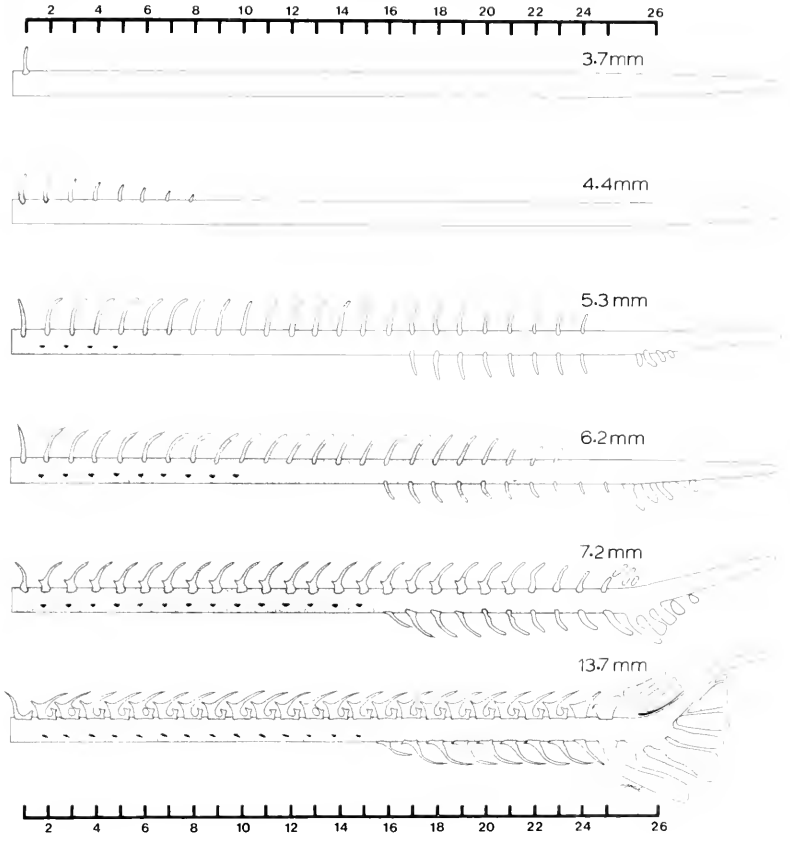


FIGURE 29.—Schematic presentation of the vertebral column development in *Xiphias gladius*. Ticks on scale denote centra number and are aligned with the middle of the centrum. Indicated millimeter measurements are ENL or ESL. Cartilage, white; ossifying, stippled.

TABLE 15.—Development of the haemal spines on the anterior to posterior numbered centra for 53 *Xiphias gladius* 5.0-6.5 mm ENL. N = number of specimens, $\bar{X}$ = mean.

Length, mm ENL or ESL	Centra with haemal spines										
	17	18	19	20	21	22	23	24	25	N	$\bar{X}$
5.0	1									1	17.0
5.1-5.5		1	1	—	1	1	4	3	8	19	23.4
5.6-6.0			1	—	2	1	2	1	9	16	23.6
6.1-6.5									17	17	25.0

larger specimens (Figs. 8, 13, 25, 27). This prezygapophysis is considerably longer than the neural spine except in large juveniles and adults (Fig. 25).

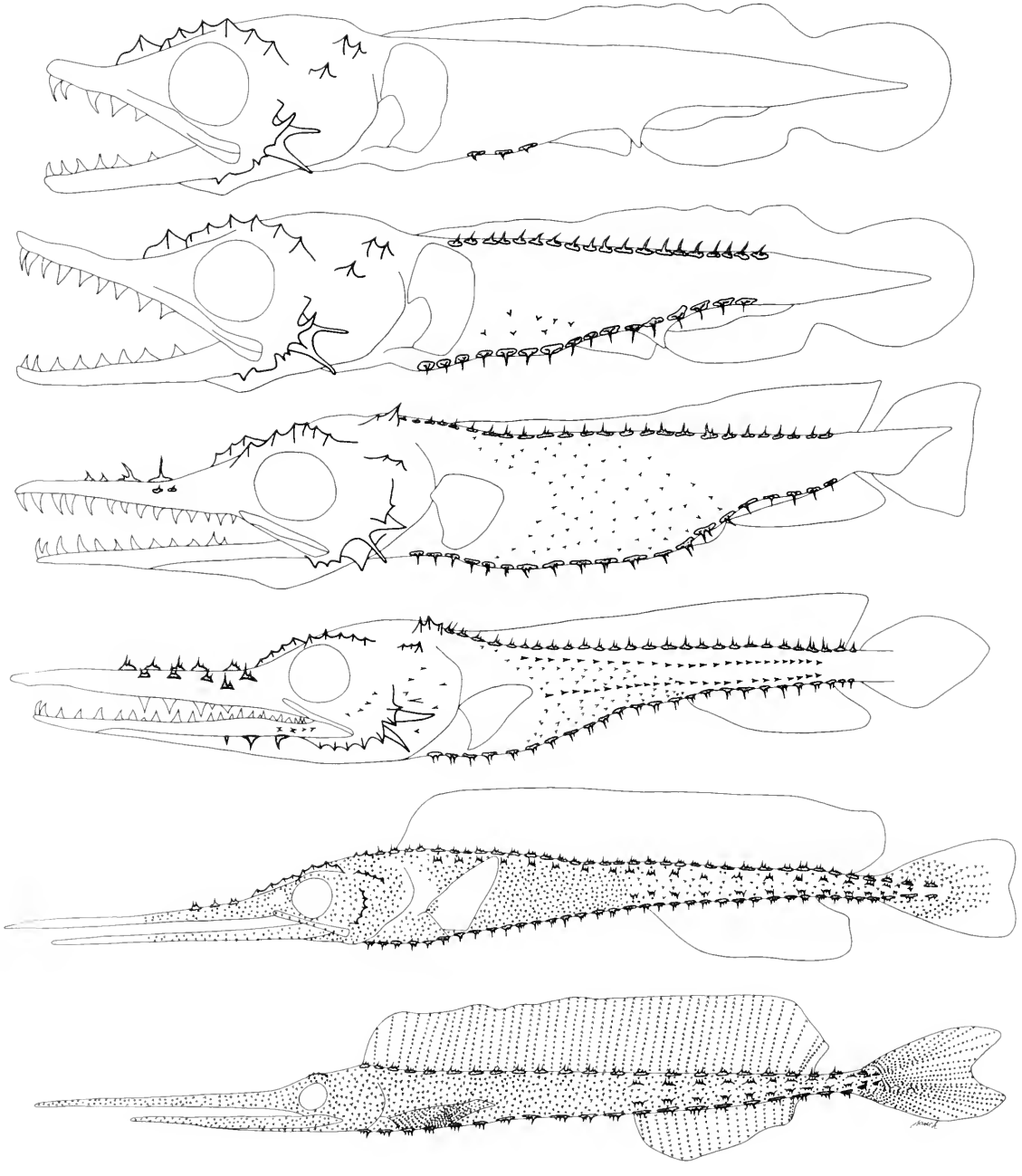
Ribs developed from a short piece of proximal cartilage. The cartilage later ossified and bone cells were added distally directly in the lengthening process of the rib during development. One pair of ribs was first seen on the anteriormost centrum at 8.0 mm ESL in some specimens. All *Xiphias* >12.2 mm ESL had at least one pair of ribs developing. Development was in a posterior direction on the first four centra and in an anterior direction on centra 15 and 14. When centra 1-3 had developing ribs, usually a pair also was present on centrum 15. Ribs developed over a wide size range. The smallest specimen with a full set of ribs on centra 1-4, 14, and 15 measured 25.1 mm ESL and all specimens larger than 55.1 mm ESL had the full rib complement. *Xiphias* usually developed ribs on centra 1-4, 14, and 15, but a few specimens also had ribs on centra 5, 6, 13, and 16.

BRANCHIOSTEGAL RAYS

Branchiostegal rays were first seen in a 4.2 mm ENL specimen and all *Xiphias* >4.2 mm ENL had some rays. The 4.2 mm ENL *Xiphias* had four rays on each side but a 4.5 mm ENL specimen had only two (Table 16). Branchiostegals were added from posterior to anterior direction. specimens with developing branchiostegals had either the same count on both sides or differed by one ray between sides. Adult counts of seven or eight rays were first observed at 5.0 mm ENL and all *Xiphias* >6.6 mm ENL had

TABLE 16.—Development of the branchiostegal rays on the left and right sides for 211 *Xiphias gladius* (3.7 mm ENL-225, 668 mm ESL). N = number of specimens, $\bar{X}$ = mean, SD = standard deviation.

Length, mm ENL or ESL	Number branchiostegal rays, left												Number branchiostegal rays, right										
	0	1	2	3	4	5	6	7	8	$\bar{X}$	SD	N	0	1	2	3	4	5	6	7	8	$\bar{X}$	SD
3.6-4.5	1	—	1	—	3	1	1			3.6	2.12	7	1	—	1	1	2	1	1			3.4	2.12
4.6-5.5					7	8	11	19		5.9	1.34	45					8	6	13	16	2	6.0	1.34
5.6-6.5							2	24	6	7.1	0.57	32							3	21	8	7.1	0.57
6.6-668								71	56	7.4	0.45	127								78	49	7.4	0.45



adult counts (Table 16). Of 127 *Xiphias* (6.6 mm ENL-668 mm ESL), 59 (46.4%) had seven branchiostegals on both sides, 37 (29.2%) had eight on both sides, and 31 (24.4%) had seven rays on one side and eight on the other.

SQUAMATION

Larvae of *Xiphias* developed four rows of scales on each side with smaller "scatter" scales between the rows (Fig. 30). First to appear between 5.3 and 6.1 mm ENL were some ventral "row" scales on the stomach. These scales were added during growth anterior to the pectoral symphysis and posteriorly to the ventral hypurals. Dorsal row scales were first seen between 5.7 and 6.9 mm ENL, approximately between the 3d and 15th centrum. The addition of dorsal row scales during growth was in an anterior direction to the top of the head and in a posterior direction to the dorsal hypurals. The two lateral scale rows were first seen in some specimens between 6.5 mm ENL and 8.6 mm ESL, extending from the posterior border of the pectoral fin to about the 16th centrum. Scales were added anteriorly only to the dorsal lateral row to about the operculum and posteriorly to the urostyle. Scatter scales, between the dorsal, ventral, and lateral scale rows first developed between 6.2 and 7.1 mm ENL on the stomach just posterior to the pectoral fin and dorsad to the ventral scale row (Fig. 30). Scatter scales, which were smaller than row scales, spread from the stomach dorsad during growth until the left and right sides in an area from the 4th centrum to the 18th centrum were covered (Fig. 30). Further addition of scatter scales was then in an anterior and posterior direction covering the whole body, the sword, and the caudal fin rays at 61.5 mm ESL, but not the pectoral, dorsal, and anal fins. In our 187 mm ESL specimen the dorsal, anal, and pectoral fin rays were covered with scatter scales. In the literature, Arata (1954); Leim and Scott (1966); Nakamura et al. (1968), and Palko et al. (1981) stated that adult *Xiphias* lack scales. Our largest 668 mm ESL specimen had scales (Fig. 31), seen through the dissecting microscope on a cleared and stained piece of skin. In this specimen the row scales could no longer be distinguished from the scatter scales.

Development of individual scales is similar for the row and scatter scales, except scatter scales start out smaller than row scales but increase in size to equal the row scales during development. Each scale starts as an oval-shaped structure with one posteriorly recurved spine. During development more posteriorly recurved spines are acquired in a row at the center of the scales and the scale margins become progressively crenated (Fig. 32). Finally, in specimens >200 mm ESL the marginal scale crenations become fewer and the recurved spines develop into blunt stubs (Fig. 32).

Individual row scales have approximately the same number of spines in a developing specimen, but this does not apply for the scatter scales. Our largest 668 mm ESL *Xiphias* had developed variable scales which had from one to seven blunt stubby spines; row scales were not distinguishable from scatter scales in this specimen (Figs. 31, 32). Arata's (1954) work on scale development agrees with our findings.

FIGURE 30.—Larval and juvenile *Xiphias gladius*, depicting the ontogeny of squamation. The size of scales was exaggerated in proportion to the body. Starting from the top and going to the bottom the specimens' lengths in millimeters are: 5.3 ENL, 6.2 ENL, 7.6 ESL, 11.5 ESL, 35.4 ESL, 188 ESL.

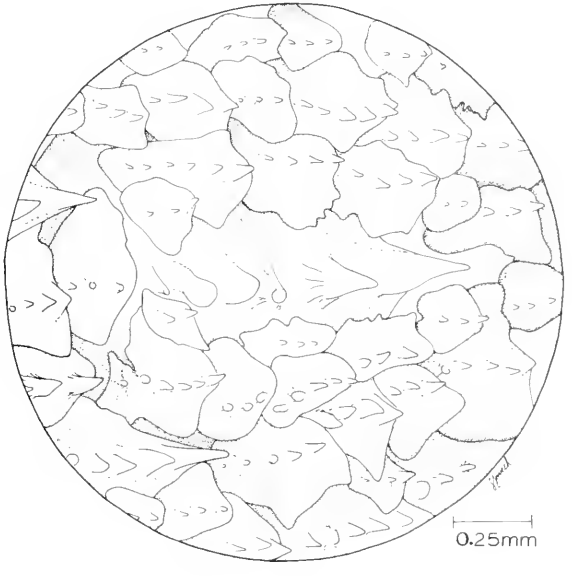


FIGURE 31.—Enlarged view of the skin from a 668 mm ESL *Xiphias gladius*, showing scales with two to six posteriorly recurved spines. White spaces between scales are skin. Anterior is to the left.

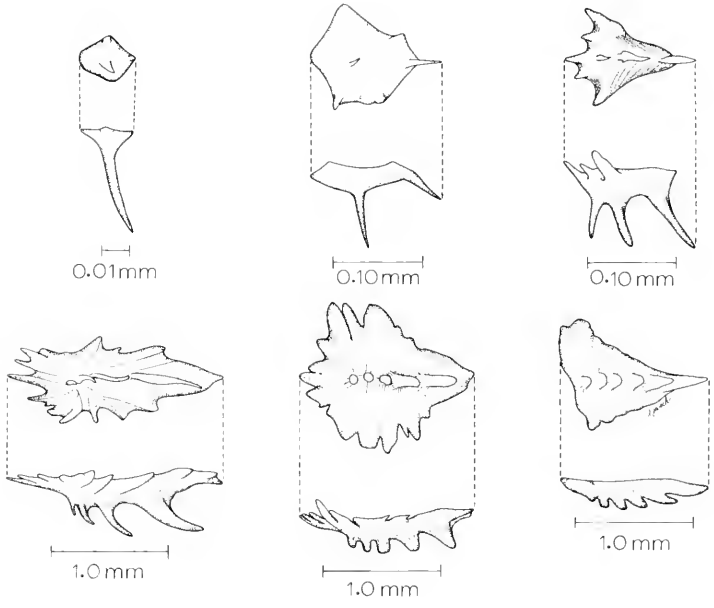


FIGURE 32.—Scales from *Xiphias gladius*, showing ontogeny. Starting from left the specimens' lengths in millimeters are: top, 5.4 ENL, 6.2 ENL, 25.1 ESL; bottom, 61.5 ESL, 225 ESL, 668 ESL. Each size in top and bottom rows has an external view (top) and a lateral view (bottom).

DISCUSSION

Xiphias gladius is a highly modified perciform fish which, in our opinion, should not be placed as the monotypic family Xiphiidae in the suborder Scrombroidei, as was done by Greenwood et al. (1966). We agree with Gosline (1968) and Fierstine (1974), who placed the monotypic family Xiphiidae under the separate suborder Xiphiioidei. However, Gregory and Conrad (1937) compared *Xiphias* bones with those of *Istiophorus* and concluded that xiphiids and istiophorids are separate but parallel families of common scombroid stock. G. David Johnson, who examined the branchial arches of *Xiphias*, istiophorids, and scombrids (unpubl. data), has evidence that *Xiphias* belongs with the scombroids. We will discuss the modifications and variations that we noted in *Xiphias* and compare these with other fish families.

The pectoral fin position in *Xiphias* larvae is lateral, but during growth to adults the fin moves ventrad to an almost pelvic position. *Xiphias* probably lost its pelvic fin during phylogeny. Remnants of a basipterygium were not found by us or other workers during development of the larvae (Yasuda et al. 1978).

Pectoral fin ray counts of the left and right sides were equal or differed by one ray in juvenile *Xiphias*. Similar results were obtained for *Archosargus* (Houde and Potthoff 1976), *Coryphaena* (Potthoff 1980), and *Scombrolabrax* (Potthoff et al. 1980). In tunas, larger differences in pectoral fin ray counts between sides were found (Potthoff 1974).

With the publication of Dingerkus and Uhler's (1977) cartilage staining technique, Fritzsche and Johnson (1980) reported the development of pectoral radials from a sheet of cartilage in *Morone*. Swinnerton (1905) reported the same for *Salmo salar* by using the "reconstruction in wax from serial sections" technique; he called the cartilaginous blade "fin-plate." We saw the same happening in *Xiphias* and labeled the sheet of cartilage "blade" (Bl) in Figure 3. It is likely that pectoral radials develop from a cartilaginous blade in all Perciformes, and perhaps all lower fishes. Starks (1930) reported a cartilaginous blade (radial plate) in adult *Dallia pectoralis* and Roberts (1981) in the salmoniform Sundasalangidae; we believe this to be an example of a neotenic structure.

The pectoral girdle in *Xiphias* is reduced as compared with a basic perciform pectoral girdle such as that found in *Coryphaena* (Potthoff 1980) and in at least some scombrids, e.g., *Sardini* (Collette and Chao 1975), *Acanthocybium* (Conrad 1938), and *Thunnus* (de Sylva 1955). In *Xiphias*, the supratemporal and intertemporal bones are absent and there is only one postcleithrum.

Adult *Xiphias* have two dorsal and two anal

fins (Leim and Scott 1966; Ovchinnikov 1970), but larvae and juveniles have one continuous dorsal and anal fin (Nakamura et al. 1951; Yabe et al. 1959). During development the fin rays in the center of the fins stop growing and the rays become subcutaneous. The subcutaneous rays and their pterygiophores are present in the adults and were dissected in our largest 668 mm SL specimen. In three scombrid genera, *Scomber*, *Rastrelliger*, and *Auxis*, we find a first dorsal and second dorsal fin separation similar to that in adult *Xiphias*, except that in these scombrids the two fins are separate initially even though the first and second dorsal fin pterygiophores are continuous (Kramer 1960; Potthoff pers. obs. on *Auxis*). There is only one anal fin in these three scombrid genera, whereas adult *Xiphias* have two anal fins.

All dorsal rays in *Xiphias* are bifurcated at their bases (Figs. 14, 15) as in *Coryphaena* (Potthoff 1980). This probably is not the case in most perciforms where the spinous rays of the first dorsal fin have a closed base with a foramen and the distal radials are situated outside the bases of the first dorsal fin spinous rays (Kramer 1960; Potthoff 1974, 1975; Potthoff et al. 1980).

The anteriormost dorsal pterygiophores in *Xiphias* insert in the second interneural space (Figs. 11, 13), as in the gempylids and trichiurids (Potthoff et al. 1980), but not as in the serranids, sparids, apogonids, scombrolabracids, and scrombrids where the anteriormost pterygiophores insert in the third interneural space (Matsui 1967; Fraser 1972; Potthoff 1974, 1975; Houde and Potthoff 1976; Fritzsche and Johnson 1980; Potthoff et al. 1980), and not as in the coryphaenids in which they insert in the first space (Potthoff 1980). No predorsal bones were present in *Xiphias*. All scombrids and most scombroids also lack predorsal bones, however some gempylids, e.g., *Ruvettus* (Potthoff et al. 1980), have one predorsal. Most other perciformes have predorsals in the first and second interneural spaces.

The first dorsal pterygiophore in *Xiphias* is variable in development (Figs. 7, 8) and originates either from one or two pieces of cartilage. In scombrids (Potthoff 1974, 1975), a two-part development of the first dorsal pterygiophore was not evidenced, but in *Morone* it was (Fritzsche and Johnson 1980).

The last (posteriormost) pterygiophore of *Xiphias* has a serially associated double ray and a stay (Figs. 9, 10). In *Xiphias*, as probably in all Perciformes, the stay develops from the proximal radial cartilage. The stay is not posteriorly bifurcated as in most scombrids (Potthoff pers. obs.), nor does it ossify into two parts as in most gempylids and some trichiurids (Potthoff et al. 1980).

Xiphias lacks middle radials as does *Coryphaena* (Potthoff 1980), whereas many Perciformes probably have middle radials at least for some of the posteriormost dorsal and anal pterygiophores (Kramer 1960; Berry 1969; Potthoff 1974, 1975; Houde and Potthoff 1976; Potthoff et al. 1980; Fritzsche and Johnson 1980).

In *Xiphias* the caudal rays are supported by only two centra (urostyle and preural centrum 2) (Figs. 17, 21, 22). This is unusual, because in most perciforms three centra support the caudal rays (Berry 1969; Houde and Potthoff 1976; Potthoff 1980; Potthoff et al. 1980; Fritzsche and Johnson 1980), and in most scombrids four or five centra support the caudal rays (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978), except in *Scomber* and *Rastrelliger* where three centra support caudal rays (Potthoff pers. obs.).

Xiphias lacks a second uroneural in the caudal complex which is present in the basic perciform caudal such as in *Archosargus* (Houde and Potthoff 1976), *Elagatis* (Berry 1969), *Scombrolabrax* (Potthoff et al. 1980), *Morone* (Fritzsche and Johnson 1980), and *Coryphaena* (Potthoff 1980), but is absent in the scombrids (Potthoff 1975). The single uroneural of *Xiphias* does not fuse to the urostyle in adults as in Thunnini and Sardini (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978), but in several specimens anomalous shapes of the uroneural were observed (Fig. 22).

We believe that *Xiphias* has lost preural centrum 3, because a centrum having an autogenous haemal spine and a neural spine with articular cartilage is lacking (Figs. 20-23). However, 1 specimen out of 164 examined with the unusual vertebral count of 16+11=27 (typical counts 15+11 or 16+10=26) had two autogenous haemal spines on preural centra 2 and 3. To our knowledge, a perciform caudal with only one autogenous haemal spine as in *Xiphias* has not been reported previously. We cannot totally rely on Monod (1968) or any other osteological descriptive work dealing only with adult fish because Potthoff (1975) showed that some autogenous hypural parts fuse during development and cannot be recognized in adults.

There is considerable fusion of caudal complex

bones in *Xiphias*. Hypurals 1-4 and the urostyle fuse to one posteriorly notched hypural plate during development (Fig. 23); the three epurals, the uroneural pair, hypural 5, and the parhypural remain autogenous, whereas in Thunnini and Sardini only one epural remains autogenous and the paired uroneural fuses to the urostyle (Collette and Chao 1975; Potthoff 1975; Collette and Russo 1978). In *Xiphias*, hypurals 1-4 develop initially from distinctly separate pieces of cartilage and fusion of the hypurals into the notched hypural plate occurs. In Scombridae a similar yet different development takes place, because in Thunnini hypurals 1 and 2 originate from one distinctly larger piece of cartilage, whereas in *Scomber* (*Pneumatophorus*), hypurals 1 and 2 originate from separate pieces of cartilage as in *Xiphias* (Kramer 1960).

The caudal rays in adult scombrids, except Scombrini, cover the whole hypural plate (Collette and Chao 1975; Collette and Russo 1978), whereas in *Xiphias* a smaller area is covered by the rays (Figs. 17, 22, 23). When the rays are disarticulated from the hypural plate in adult *Xiphias*, long vertical depressions caused by the rays can be observed on the hypural plate (Fig. 23).

Xiphias has a greater number of precaudal than caudal vertebrae (Fig. 6) (Leim and Scott 1966; Ovchinnikov 1970). The same tencency was observed in the gempylids (Matsubara and Iwai 1958; Potthoff et al. 1980) and the opposite tendency in the scombrids (Conrad 1938; de Sylva 1955; Mago Leccia 1958; Kramer 1960; Gibbs and Collette 1967; Matsui 1967; Potthoff and Richards 1970; Collette and Chao 1975). Generally, the tendency in the perciform fishes is to have a higher caudal vertebral count; the most typical count being 10+14=24 vertebrae (Johnson 1981).

The neural and haemal arches in *Xiphias* first develop distally opened (split) (Fig. 27). During development the neural and haemal arches fuse forming spines. Fusion of the neural and haemal spines proceeds from posterior in an anterior direction (Table 13). In other perciforms studied by Potthoff, split arches were sometimes observed on small larvae on the anteriormost first and second centra only, but these two arches fused to spines during development. Adult *Xiphias* retain three to six anteriormost split neural arches (Bruce B. Collette footnote 3).

Rib development and position is unique in *Xiphias*. Commonly, perciforms have pairs of dorsal (epipleural) ribs on the precaudal vertebrae starting on the first centrum and pleural ribs starting on the third centrum (Houde and Potthoff 1976; Potthoff et al. 1980). These ribs develop from anterior in a posterior direction. *Xiphias*, however, has lost many of its ribs. Generally, there are only one pair of ribs on each of the first four centra, which develop from anterior in a posterior direction and one pair on the last two precaudal vertebrae which develop from posterior in an anterior direction. We do not know if the ribs in *Xiphias* were originally epipleural, pleural, or a combination of epipleural and pleural. We were able to determine, however, the cartilage origin of ribs in *Xiphias*. Tibbo et al. (1961) stated that ribs in adult *Xiphias* are short and poorly developed, but no details on rib position were given.

An account of rib development in lower and higher fishes is given by Emelïanov (1935). He found that some bony fish develop ribs from cartilage, in others rib development from cartilage is bypassed and ribs develop directly from bone cells, and still in others, parts of the ribs develop from cartilage and other parts of the same rib develop directly from bone. In *Xiphias* the proximal portions of each rib originate from cartilage, the distal portions develop directly as bone.

The branchiostegal ray count in *Xiphias* may vary by one ray from specimen to specimen or it may vary between left and right sides in a specimen. Usually, branchiostegal ray counts are conservative and characterize fish families and sometimes genera (Kishinouye 1923; McAllister 1968; Fraser 1972; Ahlstrom et al. 1976; Kendall 1979; Matsuura 1979), however variability has been reported in some groups such as Carangidae (McAllister 1968).

We cannot make firm conclusions about the phylogenetic status of *Xiphias*. From our study we conclude that *Xiphias* is a perciform fish that differs from other perciforms to warrant the separate suborder Xiphiioidei. We were unable to determine relationship with the scombroids (gempylids, scombrids). A comparison with istiophorids remains to be done, and we believe we furnished sufficient material to facilitate such a comparison.

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AGE AND GROWTH OF LARVAL ATLANTIC HERRING, *CLUPEA HARENGUS* L., IN THE GULF OF MAINE-GEORGES BANK REGION BASED ON OTOLITH GROWTH INCREMENTS

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ABSTRACT

An estimate of the age and growth of herring larvae over their first 6 months of life is made by examining presumed daily growth increments in their otoliths. A Gompertz growth curve fitted to 311 autumn-spawned specimens collected in the Gulf of Maine-Georges Bank region describes the mean length at age (based on a range of 7-160 otolith increments) from an initial hatching size of 5.7 mm SL to a mean length of 30.9 mm at 175 days. A larva with 7 growth increments is estimated to be on average 25 days old with a mean length of 12.7 mm. Larvae reared in the laboratory at 10°C began initial increment deposition on average 4.5 days from hatching at the time of yolk-sac absorption, and the second increment was deposited an average of 12 days from hatching. The rearing experiments were terminated before an increment-day relation could be established, but the third increment was estimated to be formed on average 22 days from hatching. Support for the assumption that increment deposition becomes daily at least after the third increment is made by two independent methods. Based on the fitted Gompertz curve, average growth rates for herring larvae increased from 0.25 mm/day at hatch to 0.30 mm/day at 20 days and declined to <0.15 mm/day after 75 days of age during the winter period. This agrees closely with estimated field rates.

Atlantic herring, *Clupea harengus* L., spawn demersal eggs during late summer-autumn on the shoaler (<40 m bottom depth) regions of Georges Bank and around the perimeter of the Gulf of Maine (Bigelow and Schroeder 1953; Boyer et al. 1973; Lough and Bolz 1979[2]). Hatching occurs after 8-9 d at 10°C (Cooper et al.[3]), and shortly thereafter the larvae are dispersed throughout the water column by the vigorous tidal stirring characteristic of this region (Bumpus 1976). By following length-frequency means or modes between successive surveys, average larval growth rates have been estimated on field populations of larvae in the Gulf of Maine-Georges Bank region by Tibbo et al. (1958), Tibbo and Legaré (1960), Das (1968, 1972), Graham et al. (1972), Sameoto (1972), Boyar et al. (1973), Lough et al. (1979),[4] and others. Larval herring grow at an overall average rate of about 5 mm/mo (0.2 mm/d) from hatch (6 mm SL) to metamorphosis in the spring. Metamorphosis is a gradual transition to adult characteristics generally achieved by the time the fish are 50-55 mm, but some studies report metamorphosis occurring at much smaller lengths of 30-35 mm (Blaxter and Staines 1971; Boyar et al. 1973; Ehrlich et al. 1976; Doyle 1977).

Knowledge of larval herring growth is an important component in the estimation of age-specific mortality rates, which can be used to study variations in larval survival in relation to size of succeeding year classes. However, field estimates of larval growth only provide average rates of growth so that their use in comparative studies is limited by the sometimes polymodal length frequencies and subjective nature of connecting corresponding length modes. With the development of accurate growth models, populations can be compared by region and season with various environmental factors which may be affecting growth and hence survival of larvae. Techniques are now available for the accurate aging of larval and juvenile fishes based on

[1]Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[2]Lough, R. G., and G. R. Bolz. 1979. A description of the sampling methods, and larval herring (*Clupea harengus* L.) data for surveys conducted from 1968-1978 in the Georges Bank and Gulf of Maine areas. Northeast Fisheries Center, Natl. Mar. Fish. Serv., NOAA, Woods Hole Lab. Ref. 79-06, 230 p.

[3]Cooper, R. A., J. R. Uzmann, R. A. Clifford, and K. J. Pecci. 1975. Direct observations of herring (*Clupea harengus harengus* L.) egg beds on Jeffreys Ledge, Gulf of Maine in 1974. ICNAF Res. Doc. 75/93, 6 p.

[4]Lough, R. G., G. R. Bolz, M. D. Grosslein, and D. C. Potter. 1979. Abundance and survival of sea herring (*Clupea harengus* L.) larvae in relation to environmental factors, spawning stock size, and recruitment for the Georges Bank area, 1968-1977 seasons. ICNAF Res. Doc. 79/VI/112, 47 p.

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growth increments or lamellae in their otoliths, thus providing a detailed chronological record of events in the growth history of an individual fish (Pannella 1971, 1974; Scott 1973; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Ralston 1976; Taubert and Coble 1977; Barkman 1978; Methot and Kramer 1979; Radtke 1980[5]; Radtke and Waiwood 1980; Steffensen 1980; Wilson and Larkin 1980; Uchiyama and Struhsaker 1981; Barkman et al. 1981; Brothers 1981; Brothers and McFarland 1981; Methot 1981). Evidence for the presence of apparent daily otolith growth increments in larval herring collected along western Gulf of Maine in October 1976 was given in a preliminary report by Rosenberg and Lough.[6] Further work by Lough et al.[7] led to the development of a growth model extending through the autumn-winter period. Townsend and Graham (1981) recently used otolith aging techniques to examine the age structure of larval herring entering the Sheepscot River, Maine, estuary during autumn-winter 1978-79.

The objective of this study is to summarize our findings on the age and growth of larval herring otoliths during the first 6 mo of life, from hatching to a length of ca. 31 mm, based on larvae reared in the laboratory and collected in the Gulf of Maine-Georges Bank region. Also, a Gompertz growth curve is fitted to the length-at-age data based on "daily" growth increment in their otoliths to describe the shape of the average larval herring growth curve in this region from October through March 1976-77. The present study was initiated by the International Commission for the Northwest Atlantic Fisheries (ICNAF) (Lough et al. 1981) and the U.S. participation was conducted concurrently as part of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Center, which measures long-term changes in the variability of fish stock abundance off the northeast coast of the United States (Sherman 1980).

METHODS

Larval herring for otolith studies were collected at selected stations within a standard grid of sampling stations covering the western Gulf of Maine, Georges Bank, and Nantucket Shoals areas on five ICNAF larval herring surveys conducted from October 1976 through March 1977 (Table 1, Fig. 1). Larvae normally were collected at stations where high densities were encountered. Standard ICNAF double-oblique continuous hauls (61 cm bongo net, 0.505 and 0.333 mm mesh nets) were made at each station to a maximum depth of 100 m, or to within 5 m of the bottom in shoaler areas, while the vessel was underway at 3.5 kn. A standard haul ranges in duration from 5 to 25 min; each bongo net filtering between 100 and 1,000 m^3 of water depending on the duration (maximum depth) of the haul. Further details of the sampling gear and protocols can be found in Lough and Bolz (footnote 2). Immediately after the nets were brought aboard the vessel, larvae were sorted from the untreated 0.505 mm mesh plankton sample and frozen in dishes. Extra hauls occasionally were made to collect sufficient numbers of larvae. Tempera-

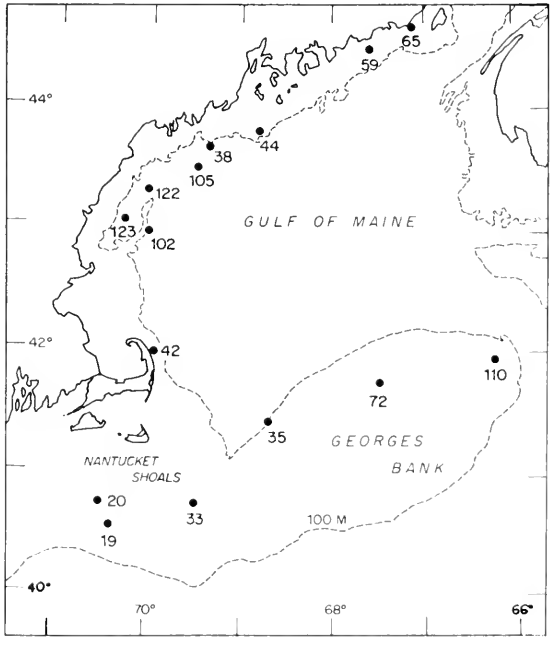

FIGURE 1.—Station locations in the Gulf of Maine-Georges Bank region where larval herring were collected for otolith aging over the 1976 spawning season.

[5]Radtke, R. L. 1980. The formation and growth of otoliths from redfish (*Sebastes* spp.) larvae from the Flemish Cap (Division 3M). NAFO SCR Doc. 80/IX/153, 6 p.

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[7]Lough, R. G., M. R. Pennington, G. R. Bolz, and A. S. Rosenberg. 1980. A growth model for larval sea herring (*Clupea harengus* L.) in the Georges Bank-Gulf of Maine area based on otolith growth increments. ICES C.M. 1980/H:65, 22 p.

TABLE 1.—Station information for larval herring specimens collected for otolith analysis by 61 cm bongo net (0.505 mm mesh) oblique hauls from autumn 1976 through winter-early spring 1977 in the Gulf of Maine-Georges Bank region.

Vessel	Cruise no.	Station	Lat. N	Long. W	Area	Date (GMT)	Time (GMT) (Night or Day)	Bottom depth (m)	Temp. (°C) at 20 m	No. larvae	Mean standard length[1] (mm)	Mean no. otolith increments[1]
Annandale	76-01	38	43°37′	69°22′	W. Gulf of Maine	8 Oct. 1976	0300 (N)	114	12.9	35	15.5 (2.7)	19.3 (6.0)
		44	43°44′	68°50′		8 Oct.	1415 (D)	76	13.0	39	14.3 (1.7)	16.0 (4.0)
		59	44°25′	67°35′		9 Oct.	1515 (D)	57	13.0	9	17.1 (2.3)	22.8 (9.3)
		65	44°36′	67°07′		13 Oct.	0330 (N)	85	12.7	37	17.5 (3.2)	23.2 (9.8)
Wieczno	76-03	72	41°45′	67°30′	Georges Bank	28 Oct.	0650 (N)	42	[2]13.8	18	14.9 (1.7)	12.1 (3.5)
Researcher	76-01	42	41°54′	69°50′	Nantucket Shoals	1 Dec.	0002 (N)	60	8.0	9	17.8 (2.4)	27.8 (10.0)
		35	41°21′	68°42′	Georges Bank	1 Dec.	0626 (N)	108	8.6	3	21.1 (0.8)	41.7 (5.9)
		102	42°58′	70°00′	W. Gulf of Maine	8 Dec.	1030 (N)	100	7.4	29	18.0 (1.6)	22.6 (7.9)
		105	43°30′	69°30′		9 Dec.	1100 (N)	150	7.5	12	18.2 (1.3)	24.4 (7.3)
		110	41°51′	66°15′	Georges Bank	11 Dec.	0955 (N)	80	8.4	37	21.3 (2.0)	44.4 (8.1)
Mt. Mitchell	77-01	19	40°33′	70°20′	Nantucket Shoals	15 Feb. 1977	0701 (N)	66	0.6	26	29.9 (2.2)	109.2 (19.0)
		20	40°45′	70°30′		15 Feb.	1026 (N)	65	0.0	2	26.7 (1.4)	87.0 (2.8)
		122	43°14′	70°01′	W. Gulf of Maine	24 Feb.	1620 (D)	124	3.5	10	26.0 (0.7)	114.6 (15.6)
		123	43°00′	70°15′		24 Feb.	1933 (D)	166	3.0	10	28.1 (2.3)	122.1 (12.8)
Anton Dohrn	77-01	33	40°45′	69°30′	Nantucket Shoals	17 Mar.	2230 (D)	47	[2]4.3	34	30.2 (2.4)	129.4 (14.0)

[1]Number within parentheses is 1 standard deviation.
[2]Only surface temperature available

ture data at each station were obtained from expendable bathythermograph traces or surface bucket readings.

Larvae were reared from fertilized eggs in the laboratory in order to determine the age at which increment deposition first begins in larval herring otoliths. A batch of herring eggs, stripped from several ripe and running adults collected along the western Gulf of Maine near Jeffreys Ledge, was fertilized on 17 October 1978 and reared at the NMFS Narragansett Laboratory at 10°C by G. Laurence for use in various feeding experiments. Larvae were maintained in special rearing aquaria described by Beyer and Laurence (1981) with a photoperiod of 12 h light and 12 h dark and fed wild plankton at high densities (>3 plankters/ml). Approximately 15 larvae were removed from the rearing aquaria daily from hatching on 28 October through 15 November and preserved in 75% ethyl alcohol.

Prior to removing the otoliths, larvae were staged according to Doyle (1977) and measured for standard length (snout to caudal peduncle) and head length (snout to sagitta in normal position) to the nearest 0.1 mm. The largest otoliths (sagittae) were removed from both sides of the head when possible and mounted in Canada balsam or Permount.[8] The otoliths were whole mounted and little difficulty was found in reading them intact so that further preparation was unnecessary. The 2-sagittae and 2-astericae obtained per individual from the laboratory-reared larvae were virtually impossible to distinguish at this early stage; however, the number of growth increments was identical for both sets of otoliths from the same individual.

The otoliths were viewed by transmitted light and growth increments were counted using a Zeiss compound microscope-video system with a magnification range of 630× for the largest otoliths and 1000× or 2000× for the smallest. Differential interference microscopy was particularly helpful in distinguishing increments of the smallest otoliths. The resolving power of our microscope is in the range of 0.2-0.5 μm. A minimum of three counts was made on all otoliths or counts were repeated until a mean value was reached with a maximum acceptable range of 5% variability. Routine otolith measurements made to the nearest micron as illustrated in Figure 2 included the following: 1) anterior-posterior di-

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

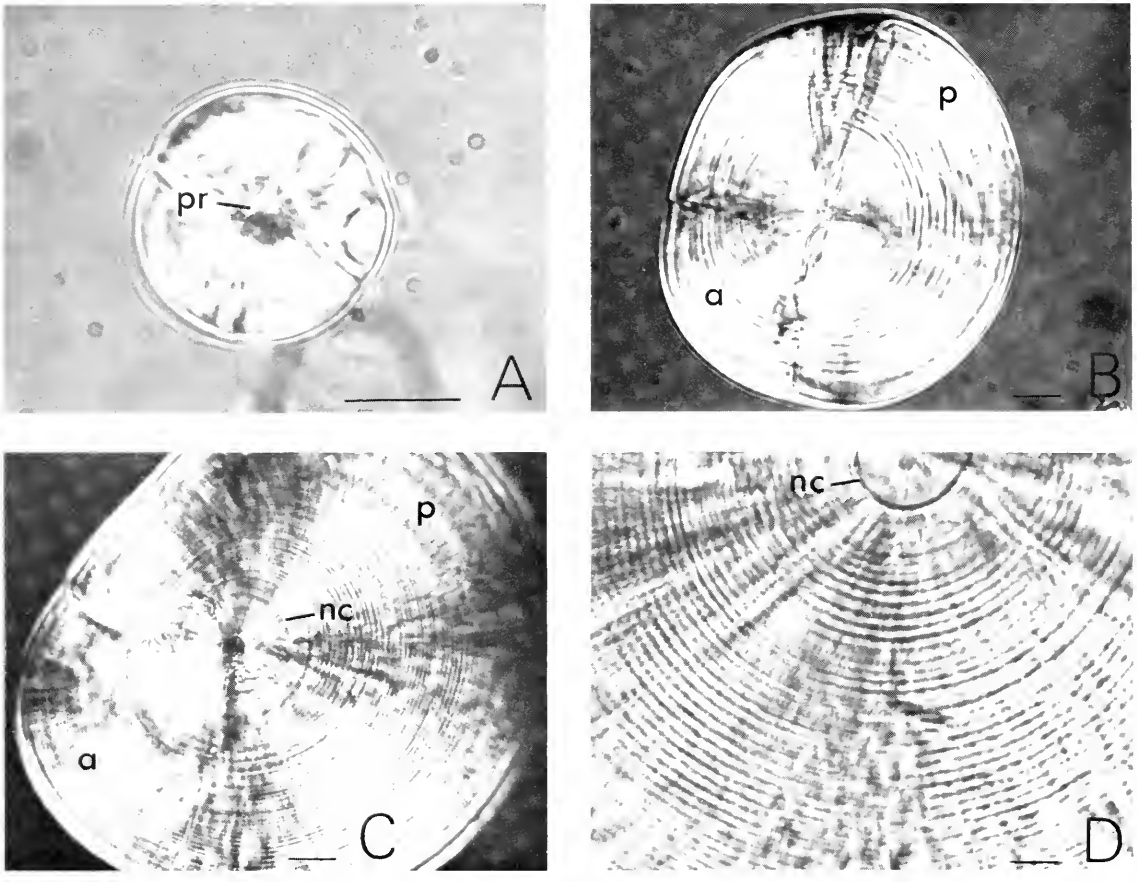

FIGURE 2.—Sagittae of herring larvae, *Clupea harengus*. Bar on photographs represents 10 μm; pr = primordium, a = anterior, p = posterior, nc = nuclear check. A. Otolith from laboratory-reared larva, 8.4 mm SL, showing 2 growth increments (1000×). Additional increments are optical artifacts. B. Otolith with 23 increments showing band of thin, poorly defined 4-5 increments around nucleus; 18.6 mm SL; *Annandale* 76-01, Stn. 38. C. Otolith with 51 increments (630×). Note the first 3-4 thin, poorly defined increments immediately surrounding nuclear check; 19.9 mm SL; *Researcher* 76-01, Stn. 105. D. Otolith with 54 increments (630×), posterior view. Note pattern of increment thickness from initial thin, poorly defined 7-9 increments encircling a heavy nuclear check increasing to maximum thickness at 10th-35th increments and then decreasing thickness towards the edge; 21.6 mm SL; *Researcher* 76-01, Stn. 35.

ameter (otolith length); 2) lateral diameter: a line perpendicular to anterior-posterior axis; 3) nucleus diameter: whole otolith at hatching without increments or to inner edge of first increment; 4) anterior radius: nucleus center (primordium) to anterior edge; and 5) posterior radius: nucleus center (primordium) to posterior edge. Selected otoliths were photographed, enlargements made, and increment thicknesses were measured across a posterior radius from the nucleus using a Zeiss MOP Digital Image Analyzer System.

All field-collected larvae used in this study for otolith aging were frozen, whereas the laboratory-reared larvae were preserved in 75% ethyl alcohol, and larvae referred to in other corroborative field studies were preserved in Formalin. Theilacker (1980) reported that the amount of shrinkage of northern anchovy larvae, *Engraulis mordax*, varies with fish size and duration of time larvae are retained within the net. Larvae smaller than 11 mm SL net-treated for 20 min could shrink as much as 19% of their live length prior to preservation. We estimate that nearly all herring larvae collected on ICNAF surveys have been dead at least 20 min prior to preservation. An additional 3% shrinkage due to 5% Formalin preservation was recommended by Theilacker

for all body parts after net-treatment, whereas preservation in ethyl alcohol (80%) did not cause any additional shrinkage in standard length. Townsend and Graham (1981) indicated that frozen herring larvae (27-45 mm TL) may shrink 3-4% more than Formalin-preserved larvae. From our experience we find that length measurements of frozen larvae can be more variable than those of Formalin-preserved larvae; however, a thorough study has not been made. No correction factor was applied to our field-collected frozen larvae because of the uncertainty of time prior to preservation and the effect of freezing on shrinkage. We do not feel that the Gompertz population growth curve fit to the uncorrected field-collected larvae would be significantly altered with respect to shape compared with corrected data. When a direct comparison is made in this paper between laboratory-reared and field-estimated larval lengths, a shrinkage correction factor applied to the lab data will be specified based on Theilacker's (1980) work which probably is adequate for all clupeidlike larvae.

RESULTS

Otoliths from 311 herring larvae caught in plankton hauls were processed in this study covering their first 6 mo of life from October through March 1977 (Table 1, Fig. 1). Approximately 58% of the larvae were collected along the western Gulf of Maine, 23% from Nantucket Shoals, and 19% from Georges Bank. ICNAF surveys have never been conducted during the month of January so that there is a gap in time in our collection of larval otolith data from mid-December 1976 to mid-February 1977. The field-collected larvae ranged in length from 11 to 35 mm with most of the western Gulf of Maine larvae falling into the 11-31 mm size range; the Georges Bank larvae, 19-25 mm; and the Nantucket Shoals larvae, 26-35 mm. The number of otolith increments counted from the field-collected larvae ranged from 7 to 160. Since we were not able to collect any recently hatched larvae <11 mm length for otoliths on these surveys, laboratory-reared larvae had to suffice for the smallest size.

Laboratory-Reared Larvae

Hatching of the laboratory-reared larvae occurred over a 5-d period with 50% hatch estimated on 28 October 1978 for a mean incubation of 11 d. Yolk-sac resorption was estimated to be 50% complete 4-5 d after hatching, and 99% complete 6 d after hatching. The larvae began actively feeding at yolk-sac resorption and appeared to be healthy without any abnormalities throughout the more than 3 wk of rearing. Mortality over the first 13 d from hatching averaged 12%/d which is considered low. The age of larvae from hatching midpoint with 0-3 increments is given in Table 2 and Figure 3. The first increment appeared on larval otoliths that ranged in age from 0 to 9 d from hatch with a middate of 4.5 d which indicates that the first increment is deposited near the end of yolk-sac resorption. Larvae staged according to Doyle (1977) showed a progression of the three substages 1a-1c over the first 3 d from hatch so that after the third day only remnants of yolk sac remained.

The second growth increment occurred in larvae 6-18+ d old with a middate of 12 d from hatch or 7.5 d from the middate of the first increment formation. The third increment was observed for the first time on a larva 16 d from hatch, but unfortunately sampling was terminated before the

TABLE 2.—Distribution of otolith growth increments, age in days from hatching midpoint, and mean standard length of herring larvae reared in the laboratory at 10°C.

Increments	Age (d) Midpoint	Age (d) Range	Mean standard length (mm)[1]	No larvae
0	3	0-6	8.0	8
1	4.5	0-9	8.1	25
2	12	6-18+	9.1	21
3	(22 est.)	16-	9.5	3

[1]Measurements made on larvae preserved in 75% ethyl alcohol. Unpreserved mean length of 55 larvae at hatch was 7.66 mm, standard deviation of 0.58 (Beyer and Laurence 1981).

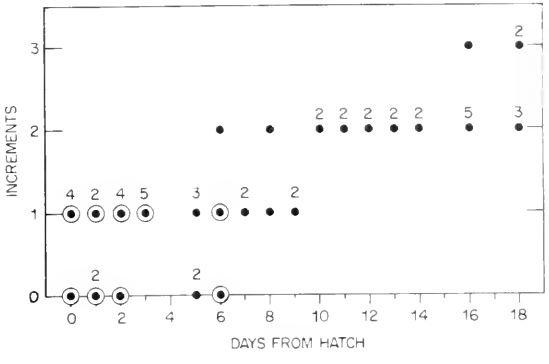

FIGURE 3.—Otolith increment deposition for herring larvae sampled from 50% hatch through 18 d of rearing in the laboratory at 10°C. Encircled points represent yolk-sac larvae. Numbers above points denote numbers of larvae >1.

complete age distribution of 3-increment larvae could be determined. If the range of ages of 3-increment larvae is similar to the 2-increment larvae, then the estimated age of 3-increment larvae would range from 16 to 28 d with a mid-date of 22 d from hatch.

Otolith Growth

The growth and morphology of young herring otoliths has been described previously by Hempel (1959) for specimens ranging in length (total) from 25 to 130 mm collected in the German Bight, by Watson (1964) for Maine herring of 85-285 mm TL, and by Messieh (1975) for Bay of Fundy herring of 32-118 mm TL. Here we describe the growth and morphology of herring otoliths (sagitta) in relation to head length for Gulf of Maine-Georges Bank larvae ranging in size from 5.7 mm (hatching) to 35 mm SL (prior to metamorphosis).

The shape of the larval herring otolith at hatching is essentially spherical having a slight convex distal side and a flat proximal side with three or four furrows radiating from a distinctive central core called a primordium (see Fig. 2). A slight protuberance is apparent on the anterior edge of the otolith from larvae starting at about 20 mm SL which develops into the adult rostrum. With further elongation along the anterior-posterior axis, the otoliths become generally pear-shaped at metamorphosis (45 mm TL) and attain the typical shape of adult herring otoliths by 75 mm (Messieh 1975). The mean diameter of the nucleus, defined here as the size of the otolith at hatching prior to increment deposition, is 22.5 μm (1.1 μm SD) based on the laboratory-reared larvae. The otolith increases exponentially in length (anterior-posterior axis) to a mean size of 456 μm at 35 mm SL based on the composite field data. Successive dark and light layers are deposited around the nucleus as the otolith grows. A single growth increment comprised of a dark plus light band is generally presumed to represent 1 d. The otolith nucleus of the field-caught larvae is readily discernible as its margin is usually darkened to form a nuclear check (see Fig. 2). In some otoliths an additional increment was seen inside of the check. Messieh and Moore[9] also have observed 1 or 2, and sometimes up to 5, faint increments inside the nuclear check of otoliths from herring larvae collected in the Gulf of St. Lawrence. However, no nuclear check was evident in otoliths of the laboratory-reared larvae and no increments were observed within the defined nucleus. Nuclear diameters of the field-caught larvae all fell within the 95% confidence limit of the mean nuclear diameter determined from the laboratory-reared larvae. Immediately surrounding the nucleus of the field-caught larvae, the first 3-9 growth increments appear to be less well defined than succeeding increments, i.e., lower optical density and thinner in width. Distinctive, darker than normal growth layers were noted across an otolith transect but they did not suggest any pattern or complex periodicity as observed by Pannella (1971), nor was there any evidence of subdaily rings as observed for some species by Taubert and Coble (1977), Brothers (1981), and Brothers and McFarland (1981). Scanning electron microscopy techniques will be necessary to resolve the presence or absence of faint increments.

The thickness of successive growth increments was measured on otoliths from three field-caught larvae along a posterior radius starting from the nucleus edge (Fig. 4). Measurements were made only through the penultimate increment in each case as the marginal increment was still in the process of formation and could not always be read clearly. Increment thickness ranged from about 0.6 to 2.4 μm along the radii. All three otoliths show the same general pattern of increment thickness up to about 23 increments where the first 7-10 increments are relatively thin (0.8-1.5 μm) and increase to near maximum thickness (2.3 μm) by about 75 increments. The thickness of the first 3 increments from the laboratory-reared larvae was consistently 0.8-1.0 μm, which compares closely with the initial increment thickness of the field-caught larvae. Otolith B tends to suggest a prolonged period of relatively thick increments before thinner ones start to be formed, whereas otolith C appears to form thin increments immediately after maximum increment thickness at around 15 increments. The form of the otolith growth curves can be seen more readily in Figure 5 where otolith radii are plotted against the number of increments for the three larvae. These curves suggest that otolith growth is initially slow, increases

[9]S. N. Messieh and D. S. Moore, Marine Fish Division, Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, N.S., Canada, B2Y 4A2, pers. commun. August-September 1981.

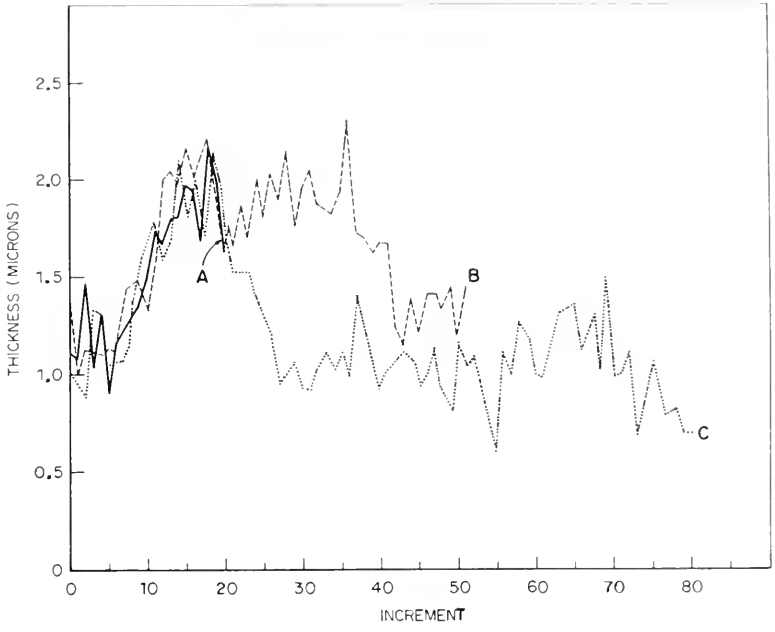

FIGURE 4.—Change in increment thickness for three field-collected herring larvae. Measurements were made along a posterior radius from nucleus edge through the penultimate increment. A. Total of 23 increments (see Fig. 2B); 18.6 mm SL larva; *Annandale* 76-01, Stn. 38. B. Total of 54 increments (see Fig. 2D); 21.6 mm SL larvae; *Researcher* 76-01, Stn. 35. C. Total of 150 increments, only initial 80 measured; 31.0 mm SL larva; *Anton Dohrn* 77-01, Stn. 33.

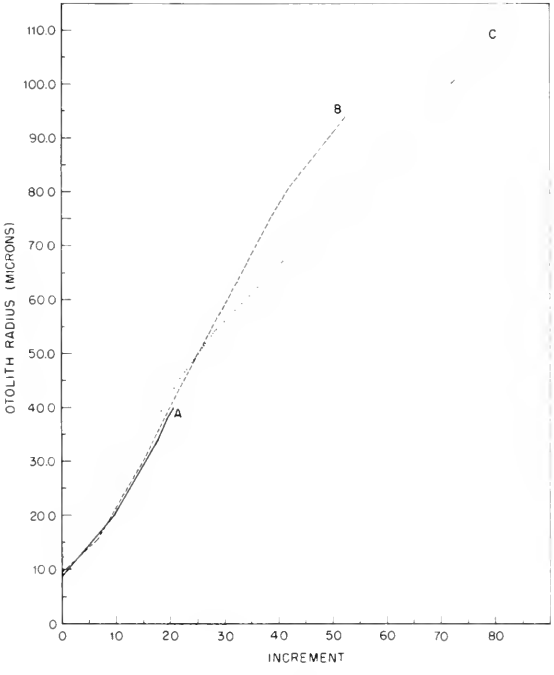

FIGURE 5.—Otolith radii vs. number of increments for the same three larvae in Figure 4.

rapidly, and then levels off at some point. This same general pattern of otolith microstructure was observed by Brothers and McFarland (1981) for French grunts.

Various allometric relations were examined between otolith size and growth of the field-caught larvae, and a few are presented here to show the homogeneity of the measurements from the three spawning populations sampled: western Gulf of Maine, Georges Bank, and Nantucket Shoals. A plot of the otolith anterior vs. posterior radii in Figure 6 shows a linear relationship. The posterior radius becomes increasingly longer than the anterior radius with increment deposition. Otolith length plotted against head length

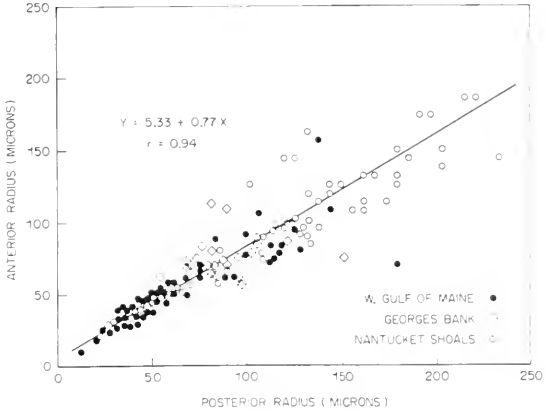

FIGURE 6.—Otolith anterior-posterior relation for herring larvae collected from the three areas: western Gulf of Maine, Georges Bank, and Nantucket Shoals, with composite regression line and correlation coefficient (r).

in Figure 7 also can be expressed by a simple linear relationship. The long axis of the otolith shows a positive allometry with respect to head length for recently hatched larvae to a size of about 35 mm SL. Hempel (1959) reported nearly isometric growth between head and otolith length after metamorphosis for German Bight herring.

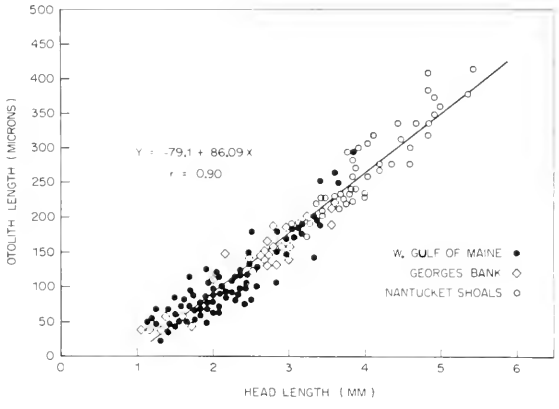

FIGURE 7.—Otolith length (anterior + posterior radii)-head length relation for herring larvae collected from the three areas: western Gulf of Maine, Georges Bank, and Nantucket Shoals, with composite regression line and correlation coefficient (r).

Larval Growth

A composite plot of larval length versus number of otolith increments is presented in Figure 8. A Gompertz growth curve was fitted to the field data to produce a description of the mean growth of larval herring based on the 311 specimens with otolith growth increments ranging from 7 to 160. The Gompertz-type curve (Laird 1969) has been used to describe growth of a wide variety of organisms that often grow exponentially at a rate which is decaying exponentially. Previous use of the Gompertz model to more accurately describe the growth of young fish has been made by Kramer and Zweifel (1970), Sakagawa and Kimura (1976), Zweifel and Lasker (1976), and Methot and Kramer (1979). Using the field data as a starting point, it was assumed that increments were deposited daily at least after the 7th increment so that the equation

$$L = L_7 \exp[k(1 - \exp[-\alpha(r - 7)])], \quad r \geq 7,$$

was taken to represent mean larval length as a function of age where r, the number of increments, represents age plus some unknown constant (see Pennington 1979 for details of the model fit).

The fitted equation was found to be

$$L = 12.70 \exp[0.89(1 - \exp[-0.03(r - 7)])] \quad \text{for } r \geq 7, \quad (1)$$

where $12.70 = L_7$, the mean length of a 7-increment larvae.

Equation (1) may be rewritten as

$$L = 30.90 \exp[-1.07 \exp(-0.03\ r)], \quad r \geq 7, \quad (2)$$

where $30.90 = \hat{L}_\infty$, the asymptotic limit of mean growth during the October-March period. Assuming: 1) for at least $r \geq 7$, increments are deposited daily and 2) a curve in the form of Equation (2) approximates growth from hatch, then denoting age by x,

$$x = r + c, \quad r \geq 7,$$

from 1), where c is an unknown constant, or

$$r = x - c, \quad x \geq c + 7.$$

Thus

$$L = 30.90 \exp(-1.07 \exp[-0.03(x - c)]), \quad x \geq c + 7, \quad (3)$$

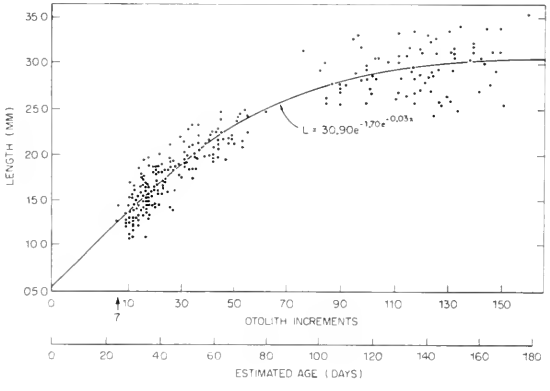

FIGURE 8.—Composite standard length-otolith increment plot for field-collected herring larvae in the Gulf of Maine-Georges Bank region, October 1976-March 1977. A Gompertz curve is fitted to larval length at estimated age, x, over their first 6 mo of life from a mean hatch length of 5.7 mm to an asymptotic limit of mean growth of 30.9 mm. A larva with 7 otolith increments is estimated to be on average 24.8 d old. See text for details.

which, if assumption 2) is reasonable, Equation (3) holds for $x \geq 0$. Letting L_0 denote mean length at hatch ($x = 0$), then solving Equation (3) for c yields,

$$c = \frac{\text{Ln}(3.431 - \text{Ln } L_0) - 0.065}{0.026} .$$

Table 3 gives an estimate of the age of larvae with 7 increments (24.8 d) derived from the mean length of recently hatched larvae collected on the Jeffreys Ledge spawning beds (Cooper et al. footnote 3).

When the mean hatching size (L_0) = 5.7 mm, c = 17.8 d, and from Equation (3), length as a function of age is given by

$$L = 30.90 \exp[-1.70 \exp(-0.03\ x)], \quad x \geq 0. \quad (4)$$

From Equation (4) the mean length at age along with 95% confidence limits, and growth rate (millimeters/day) are estimated from the time of hatch through 175 d in Table 4. Also, the fitted growth curve is shown in Figure 8 with the estimated larval age referenced to the lower scale. The growth curve is based on data with more than 6 increments and a mean length of 5.7 mm at hatch. Obviously, if the functional form changes between age 0 and the age corresponding to 7 increments, then the predicted age of fish with 7 or more increments is biased.

This growth curve is based on larvae that survived to the age when caught. Therefore, the back-casted curve represents the mean length of larvae for a given age which survive and hence, may be higher than the mean length of the total population.

The mean lengths at age of laboratory-reared larvae having 1 and 2 increments from Table 2 fall reasonably close to the extrapolated curve near the origin. The mean length of the laboratory-reared larvae at hatch was reported by Beyer and Laurence (1981) to be 7.66 mm (SD = 0.58 mm). After correcting for a 20-min net-treatment and Formalin preservation shrinkage factor to compare with the field data, their reported mean hatching size is estimated to be 6.4 mm, which is not significantly different from the Jeffreys Ledge diver-collected, Formalin-preserved yolk-sac larvae of 5.7 mm mean SL.

An estimate of $\sqrt{\text{var}(x|r)}$, the standard deviation of age for a fixed number of increments, was made from the field data by Pennington (1979), and its value of 2.9 d compares closely with the rough estimate of 3.1 d obtained from the laboratory data (Lough et al. footnote 7).

TABLE 3.—Age of larval herring with 7 otolith growth increments estimated from an initial mean hatching size of 5.7 mm (0.54 mm SD) and 95% confidence intervals of the mean. Standard lengths of 100 newly hatched yolk-sac larvae (Formalin[1] preserved) were measured from egg bed samples collected by divers[2] on the Jeffreys Ledge study site (38 m depth), 8 October 1974.

Hatch length (L_0) (mm)	95% confidence intervals		Estimated age of larva with 7 increments (d)	95% confidence intervals	
	lower	upper		lower	upper
5.7	5.6	5.8	24.8	24.4	25.2

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.
[2]Northeast Fisheries Center's Manned Undersea Research and Technology (MURT) Dive Team

TABLE 4.—Mean standard length at age, 95% confidence limits, and growth rate (mm/d) of larval herring from hatch through 175 d estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% confidence limits		Growth rate (mm/d)
		lower	upper	
0	5.7	5.4	6.0	0.25
1	5.9	5.6	6.2	0.26
2	6.2	5.9	6.5	0.26
3	6.4	6.2	6.7	0.26
4	6.7	6.4	7.0	0.27
5	7.0	6.7	7.3	0.27
6	7.2	6.9	7.5	0.27
7	7.5	7.2	7.8	0.28
8	7.8	7.5	8.1	0.28
9	8.1	7.8	8.4	0.28
10	8.4	8.1	8.7	0.29
20	11.3	11.0	11.6	0.30
30	14.2	14.0	14.5	0.29
40	17.0	16.8	17.2	0.27
50	19.5	19.3	19.7	0.23
75	24.3	24.0	24.6	0.15
100	27.3	26.8	27.7	0.09
125	29.0	28.4	29.5	0.05
150	29.9	29.3	30.5	0.03
175	30.4	29.8	31.0	0.01

The first larva with 3 increments observed during the laboratory-rearing occurred on day 16 after estimated hatch. The mean age of fish with 3 increments cannot be estimated directly because sampling stopped after 18 d. But assuming a range of ages of 12 d (4 standard deviations), the mean age of a 3-increment larva would be approximately 22 d. Assuming daily increment deposition for the population after the third increment, a 7-increment larva would have an average age of 26 d, which compares well with the field estimate of 25 d.

Messieh and Moore (footnote 9), working with autumn-spawned herring larvae in the Gulf of St. Lawrence, recently estimated the age of larvae at the time of the nuclear check completion to be 15-17 d from hatching on average.

Growth Curve Compared with Other Field Studies

Direct observations of herring egg beds by divers were made on Jeffreys Ledge, Gulf of Maine, in 1974 by Cooper et al. (footnote 3). Spawning occurred between 29 September and 3 October 1974 at about 35-50 m depth when the bottom water temperature was 9.6°C. Larval hatching began on this site on 6 October and was completed by 11 October, a 5-d period. Careful visual examination of the egg bed by the divers suggested that major hatching began on 7-8 October. Newly hatched larvae collected on the egg bed have already been reported in Table 3 to have a mean Formalin-preserved length of 5.7 mm (0.5 mm SD). A special 24-h vertical series of plankton hauls was made slightly downstream of the egg bed 11-12 October (*Delaware II* 74-12). The mean Formalin-preserved length of all larvae collected by day and night hauls was 6.7 mm (0.6 mm SD) (Lough and Cohen[10]). Approximately 4 d transpired between the middates of maximum hatching and their collection by the 24-h vertical study yielding an average growth rate of 0.25 mm/d. According to the fitted Gompertz growth curve (Table 4), 4-d-old larvae are estimated to have reached a mean length of 6.7 mm at a mean growth rate of 0.26 mm/d (range: 0.25-0.27 mm/d) which are essentially the same as the field estimates.

Graham and Chenoweth (1973) made direct observations of larval herring over egg beds on northeastern Georges Bank during autumn 1973. Submersible observations indicated that hatching occurred between 25 September and 5 October, a 10-d period. Larvae hatched in seawater from eggs brought on shipboard 27 September varied in length from 5 to 7 mm with over 90% at 6 mm. On 1 October, larvae collected within the vicinity of the egg beds varied from 5 to 9 mm in length but the mean was 7.1 mm about 4 d from hatching (27 September-1 October). Growth rate of these recently hatched larvae over the 4 d was estimated to be 0.28 mm/d, which is slightly higher but still comparable with the fitted growth curve.

Growth of larval herring based on the Gompertz curve was 0.25 mm/d at hatch, increased to 0.30 mm/d at 20 d, and declined thereafter to <0.15 mm/d after 75 d. The average growth rate over 150 d from hatch was 0.20 mm/d which is similar to average seasonal estimates found in most other studies of herring larvae. By following length-frequency modes for Georges Bank-Nantucket Shoals herring larvae collected on the 1971-78 ICNAF surveys, Lough et al. (footnote 4) found an average rate of 0.195 mm/d as the best compromise to describe average growth over the 7-30 mm size classes (163 d). Boyar et al. (1973) estimated larval herring growth in the Georges Bank-Gulf of Maine region, September-June, to average 0.17 mm/d with a range of 0.14-0.25 mm/d. The form of the growth curve appears to be universal for herring larvae with a cessation in growth most noticeable during mid-larval life before increasing rapidly again at the time of metamorphosis. When Sette (1943) replotted the Clyde Sea, spring-spawned larval herring data of Marshall et al. (1937), he concluded that two logarithmic curves provided a better description of growth with a decrease in slope at a length of 19.5 mm. Graham et al. (1972) also showed a decrease in growth after about 20 mm for autumn-spawned herring larvae along the coastal western Gulf of Maine. Townsend and Graham (1981) followed two groups of larvae that entered the Sheepscot River estuary of Maine that grew about 0.2-0.3 mm/d from October to early January and from late February to early March, but experienced similar cessation of growth from late January to early February. Das (1968, 1972) followed length modes of Bay of Fundy-Gulf of Maine area herring larvae from hatching in September and estimated growth rates to be 0.29 mm/d in the autumn, gradually declining to <0.14 mm/d during late autumn and winter months, and then increasing geometrically to >0.36 mm/d in the spring and early summer. Messieh and Moore (footnote 9) also reported a rapid increase in growth at metamorphosis for herring larvae collected in the Gulf of St. Lawrence.

DISCUSSION

The available data indicate that the age and growth of herring larvae in the Gulf of Maine-Georges Bank region can be accurately estimated from otolith microstructure, although we have no direct evidence of the increment-day relation. A Gompertz growth curve fitted to the

[10]Lough, R. G., and R. E. Cohen. 1982. Vertical distribution of recently-hatched herring larvae and associated zooplankton on Jeffreys Ledge and Georges Bank, October 1974. Lab. Ref. 82-10. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

field-caught larvae, which describes the length at age from an initial mean hatching size of 5.7 mm to an upper asymptotic mean length of 30.9 mm, agrees well with average growth rate estimates from other studies. Our field data begin with a 7-increment larva of 12.6 mm SL, which also is nearly identical to the mean length at increment age estimated by the growth curve. From the growth model a 7-increment larva is estimated to be on average 25 d from hatch (5.7 mm) having grown at an average rate of 0.28 mm/d. This implies that increment deposition does not occur daily over these 25 d or that variation in the timing of first increment deposition is high. If one assumes daily increment deposition from yolk-sac resorption (4.5 d), a 7-increment larva would be 11.5 d old, inferring the larva has grown at an average rate of 0.60 mm/d, which is rather high based on field and laboratory estimates. Herring larvae <15 mm have estimated growth rates typically in the range of 0.25-0.30 mm/d with an upper limit of about 0.35 mm/d.

The apparent delay in increment formation observed in the laboratory-reared herring larvae after the first increment at yolk-sac resorption may be due to rearing conditions, although we have no reason to suspect they were less than optimal. Other studies have shown that the formation of daily growth increments can be affected by variations in food ration, temperature, light-dark cycle, age of fish, and stressful conditions in general (see references in first section of paper). Increment formation appears to be species-specific and, for clupeoid species like *Engraulis mordax* (Brothers et al. 1976) and *Clupea harengus* (this study) with relatively small eggs and short incubation period, the initial increments begin at the time of yolk-sac resorption (Radtke and Waiwood 1980). A dark band or check observed around the nucleus of most of the larval otoliths collected in the field, but not apparent in the laboratory-reared larvae, may correspond to the time of yolk-sac resorption as Radtke and Waiwood (1980) found for larval cod otoliths. The nuclear check may be the result of several thin increments grouped together. Uchiyama and Struhsaker (1981), working with Pacific tunas, found that countable growth increments were formed only when the fishes were fed to satiation throughout the day. The nuclear check and the succeeding 10 or so thin increments observed for the field-caught herring larvae may be related to the inability of a first-feeding larva to meet its maximum daily ration during the transition from its yolk supply to exogenous feeding. Initial feeding efficiency is low for herring larvae, <5% success at yolk-sac resorption, but increases to about 40% 2 wk after hatching and 70% after 5 wk (Blaxter and Staines 1971). Farris (1959) observed a rapid leveling off of growth after hatch in four species of fish and Zweifel and Lasker (1976), after fitting a two-stage Laird-Gompertz growth curve to a number of larval fish species, one from hatching to yolk-sac resorption and another to more rapid growth at the onset of feeding, suggested that this phenomenon was almost universal in larval growth. It is conceivable that during this period of reduced growth, increment deposition also may be delayed or diminished until the larva learns to capture sufficient numbers of prey and begins growing rapidly again.

Although larval herring appear to be very resistant to the range of temperatures normally encountered (Blaxter 1960), the effect of temperature on increment formation is not known. Water temperatures observed in herring spawning areas in the Gulf of Maine-Georges Bank region are typically as high as 12°-14°C in early autumn and decline to near 0°C in winter (Table 1), approaching their lower lethal limit (Graham and Davis 1971; Chenoweth 1970). Yolk-sac utilization in herring larvae is directly related to water temperature (Blaxter 1956; Blaxter and Hempel 1963, 1966; Blaxter and Ehrlich 1974) and variations in water temperature at hatch can reduce or extend the time to first feeding and consequently, otolith increment formation. Yolk-sac resorption is completed at 4-5 d at 10°C and 6 d at 8°C. Feeding of larvae is believed to commence at or prior to the end of yolk-sac resorption when the maximum body weight (excluding yolk sac) is reached after about 3 d at 8°C and 2 d at 12°C. Larvae reared at 10°C would initiate feeding 2-3 d after hatch. There is some evidence to indicate that early larval herring growth is better at higher temperatures (Blaxter 1962), although food availability is considered the more important factor in controlling growth processes and survival of larval fish in general (May 1974). Increment formation of the green sunfish, *Lepomis cyanellus*, could be stopped when growth was slowed sufficiently by simulated winter conditions (Taubert and Coble 1977). The slowing of growth during the winter period observed for larval herring in the Gulf of Maine-Georges Bank region also may affect their increment formation but further research will be required to

determine the effect of environmental variables on the relationship between otolith and larval growth.

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INCREMENT FORMATION IN THE OTOLITHS OF EMBRYOS, LARVAE, AND JUVENILES OF THE MUMMICHOG, *FUNDULUS HETEROCLITUS*[1]

R. L. RADTKE[2] AND J. M. DEAN[3]

ABSTRACT

The formation of otoliths and the effect of light cycles on increment formation were studied in embryos, larvae, and juvenile mummichogs, *Fundulus heteroclitus*. We found that increments in the sagitta of mummichogs were a reliable indicator of the daily age of the fish. Calcification of the sagitta was initiated in the core, after matrix formation, at stage 24 of embryological development. The sagitta was the first calcified tissue to develop and there were two or three increments formed before hatching. Daily increment formation in the sagitta was initiated by light and controlled by a 24-hour photoperiod. When embryos were subjected to a 24-hour dark or <24-hour (6L:6D) photoperiod, daily increment formation was disrupted. Laboratory experiments at 24°C and 30°C confirmed that there was one increment formed each day, which was independent of growth rate and which validated the age of fish in field collections. Wild populations reproduce in the intertidal zone, a physically stressed environment and, judging by the age, which was estimated from incremental data, reproduction is synchronized with tidal cycles.

Interpretation of increments in the hard tissues of fish has long been utilized as a method to estimate age composition of adult populations. Most of the interpretive emphasis has been placed on otoliths and scales. However, the process of age determination is not a simple one (Bagenal 1974). Otoliths are especially useful for determining the age of fishes, such as larval forms, which lack scales or have very small ones.

The otoliths of teleosts consist of deposits of calcium carbonate in the form of aragonite (Irie 1955; Degens et al. 1969). The morphology of these structures is so specific it can be used as a taxonomic character (Messieh 1972; Hecht 1978). Three structures (the sagitta, lapillus, and the asteriscus) are found in the membranous labyrinth of inner ear on each side of the brain cavity (Lowenstein 1971; Popper and Coombs 1980). The sagitta is often the largest and is most often used for age determinations and, unless otherwise stated, was the otolith used in the present study.

Pannella (1971, 1974) postulated that daily increments are found in otoliths of adult fishes, and Brothers et al. (1976) showed that such increments can indeed be found in otoliths of young fishes and be used for age estimation. Struhsaker and Uchiyama (1976) postulated that back calculation of daily increment data from otoliths could be used to age the nehu, a tropical marine fish, and Ralston (1976) obtained similar results with a tropical butterfly fish. Taubert and Coble (1977) did direct age observations of otoliths in juvenile freshwater fish and Barkman (1978) was equally successful with the young of a temperate estuarine species *Menidia menidia*. A more accurate daily journal is available in the otoliths of most young fishes than can be found in their scales, since scales are often absent in the early stages of development (Bagenal 1974), and scale metabolism is dynamic (Yamada and Watabe 1979).

The discovery of daily increments in otoliths increases the resolution and precision of age determination and promises to provide fishery biologists with new levels of information. The deposition of the increments in a rhythmic fashion could be a mark of a daily event, and possibly a measure of growth, but the full extent of the influence of external and internal factors on the formation of otolith increments has not been determined.

There is need of knowledge about the age com-

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position of larval fish populations, since this information can provide estimates of growth, mortality, and rates of survival (Gulland 1977). The highest mortality of fishes is during the growth period from larvae to juveniles (Hjort 1914; Tanaka 1972) and consequently, the survival and growth of larval fishes has a pronounced effect upon recruitment (Larkin 1978). It should be possible, by using otoliths for estimation of the age, to determine the growth rates and the age structure of larval fish populations.

Daily increments have been correlated with natural temperature cycles, light and food for freshwater species by Brothers (1978, 1980[4]). Taubert and Coble (1977) postulated that daily increments in otoliths of freshwater sunfish resulted from a 24-h diurnal light cycle that entrained an internal clock.

To utilize daily depositional increments of the otoliths in the analysis of fish population dynamics, it is important to understand the physiological mechanisms involved in the formation and growth of increments and otoliths. Age estimation requires knowledge of 1) age when increment formation begins; 2) factors which control the deposition of daily increments in the otoliths; and 3) length of time daily increments are formed without growth interruption. Information in these areas will make it possible to better understand age and growth in wild populations of fish.

An important area for research in the field of age and growth is the experimental study of the factors which influence the deposition of increments in otoliths. Brothers et al. (1976) showed that daily increments began to form at different ages in different species. Some species hatch with increments already formed, while others apparently do not form increments until later. Thus, it is necessary to study the formation of increments in each species and correlate increment formation with external factors before accurate age determinations can be made.

The mummichog, *Fundulus heteroclitus*, is an abundant estuarine fish and an important component of the estuarine ecosystem (Cain and Dean 1976; Valiela et al. 1977; Kneib and Stiven 1978; Merideth and Lotrich 1979). The biology of *Fundulus* is well-known and its embryology is well-defined (Armstrong and Child 1965).

The objectives of this study were to 1) delineate the structure and formation of otoliths in the embryological and early larval stages of the mummichog, 2) determine the effect of photoperiod on increment deposition in embryonic and postlarval mummichog otoliths, 3) measure the effects of temperature on body growth and the deposition of increments in otoliths, and 4) test whether growth and age data can be obtained in wild populations of mummichogs by counting the increments in otoliths.

METHODS

Adult *F. heteroclitus* used as spawning stock were collected from North Inlet Estuary (lat. 32°20′N, long. 79°10′W) and North Edisto Estuary (lat. 32°26′N, long. 80°12′W), near Georgetown, S.C. Fertilized eggs were collected as previously described by Middaugh and Dean (1977). Only embryos which developed according to the criteria of Armstrong and Child (1965) were utilized in the embryological studies, and only larvae which hatched within 6 h of hatch induction were used in the growth studies. The embryo is the stage from fertilization to hatching; from hatching to yolk-sac absorption is the larval stage and the mummichog was considered a juvenile after yolk-sac absorption (Hubbs 1943).

The terms used to describe growth increments in otoliths are confused, as the increments in larvae are variously referred to as lamellae, rings, or layers. The term increment in this study refers to a unit formed by an unbroken incremental zone and a discontinuous zone after core formation (Fig. 1), Wild and Foreman (1979).

Newly hatched larvae were kept at 24°C and 30°C±1°C (Radtke and Dean 1979) and were fed brine shrimp, *Artemia* nauplii, ad libitum and maintained in L12:D12 with a daily change of water (30‰) to determine the effect of the rate of growth on otolith size and increment number.

A daily sample of 10 larvae was collected for laboratory experiments from each group for the first 10 d, and every 5 d thereafter for 30 d. Standard lengths (SL) were measured on each larva and its otoliths were removed. Photomicrographs were made of each otolith for increment counts.

Juvenile mummichogs were collected from We Creek in North Edisto Estuary on 9 June 1977 (28°C, 29‰). Each fish was weighed, measured for standard length (SL), and its otoliths extracted for increment counts from photographs. Statistical analyses of the data were done with

[4]E. B. Brothers, Section of Ecology and Systematics, Cornell University, Ithaca, NY 14850, pers. commun. October 1980.

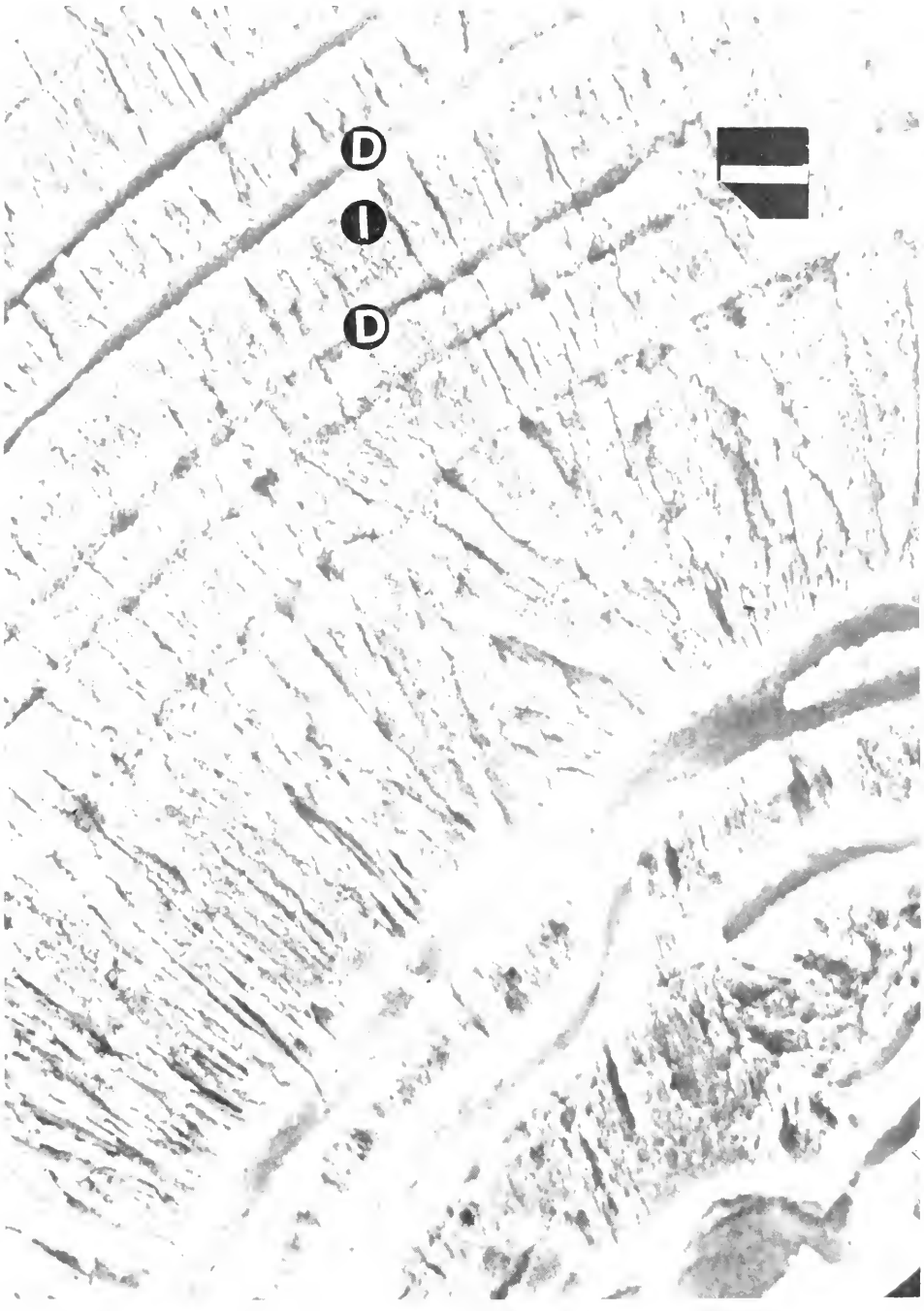

FIGURE 1.—SEM of the sagitta from a 12-d-old *Fundulus heteroclitus*. I is the unbroken incremental zone, D is the discontinuous zone, and I + D = 1 increment. Bar = 1 μ.

standard tests and models as described in Sokal and Rohlf (1969).

Removal, Preparation, and Inspection of Otoliths

Otoliths were removed from embryos, larvae, and juveniles with fine insect needles mounted on wood rods. The larvae are transparent and the otoliths are birefringent under polarized light, so it is possible to view the sagitta during the dissection. The sagittae were washed with distilled water, dried, and mounted on glass slides with Euparol[5] mounting medium, and viewed with a compound light microscope.

Photomicrographs were made of each otolith for counts of increments and measurement of otolith diameters. (The I of the outside edge of the sagitta was considered as a portion of the last increment.) To make increment counts, the back of each photograph was marked and the photographs were shuffled. The counting process was performed three times, which gave three unbiased readings for each otolith. If two of the counts were identical, that value was accepted as the increment count for a particular otolith. In cases where all counts differed, the middle count was chosen unless all counts varied more than two increments from each other, in which case that otolith was disqualified and not used in the final tabulation. Sagitta were measured at the widest diameter on the photographs using a caliper calibrated on a photographed micrometer.

Sagittae viewed with light microscopy showed fine lines in the I that were concentric with the D; these fine lines have been referred to as "subunits." In the otoliths of young mummichogs the so-called subunits could not be observed in decalcified sections with light microscopy or SEM (Fig. 1). The D and I compose an increment and are readily differentiated with light microscopy in *Fundulus* sagittae (Fig. 2).

Whole sagittae used for SEM studies were attached to viewing stubs in 5-min epoxy resin. The sagittae were ground to the core in the transverse plane on graded grinding stones, polished with diamond-polishing compound, and cleaned with 95% ethanol. The polished surface was decalcified with 7% EDTA (pH 7.4) (disodium ethylenediaminetertacetate) for 1 to 5 min. The specimens were coated with gold (150A) and observed with a SEM.

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

Embryological Formation of Otoliths

Fertilized eggs were kept in light 12 h and in the dark 12 h (L12:D12) at 24°C in hatching jars with recirculating seawater (30‰). A sample of 10 eggs was collected each day until hatching and viewed under polarized light (120×) to determine when calcification was initiated. The embryos were classified according to Armstrong and Child (1965) with the number of embryos with calcified sagitta noted in each stage.

Calcified sagittae were removed from the embryos and mounted for examination with light microscopy to determine the time of increment formation. Ten- and 14-d embryological sagittae were viewed using SEM to confirm the light microscope observations.

Effect of Light on Increment Formation in Embryos and Larvae

To determine the influence of light on increment formation, developing embryos and larvae were subject to the following conditions:

EMBRYOS:

Group ED24—Embryo-dark-24 h, fertilized in the dark, kept in constant darkness until sampled 3 d after hatching.

Group EL24—Embryo-light-24 h, fertilized in the light, kept in constant light until sampled 3 d after hatching.

Group ED24+L—Embryo-dark-24+L, fertilized in the dark, kept in constant darkness except for 1 min of light exposure 10 d after fertilization. Sampled 3 d after hatching.

Group EL12:D12—Embryo-light-12 h:dark-12 h, fertilized, placed in L12:D12 and sampled daily.

All groups were maintained at 24°C and the water (30‰) was changed daily. The water was changed in the ED24 group and ED24+L group by pouring the eggs onto a 505 μ mesh net mounted on the end of 10 cm plastic tubing. The eggs were then washed off the netting with a wash bottle and the entire exercise was performed in total darkness. Hatching in the ED24 group and ED24+L group was determined by touch, because embryos are hard and easily distinguished when they have hatched. A daily

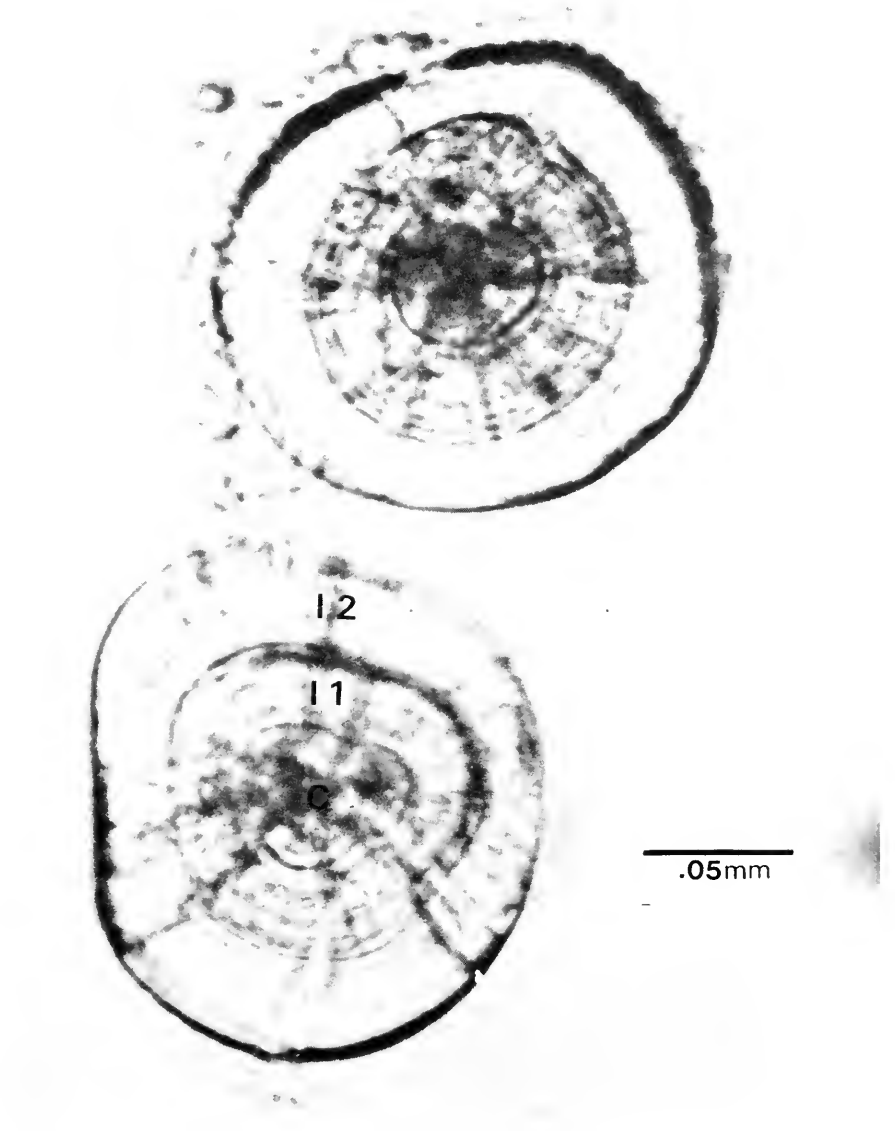

FIGURE 2.—Light micrograph of a *Fundulus heteroclitus* sagitta on the day of hatching. C is the core and I1 and I2 are increments formed after core formations but prior to hatching. Bar = 0.05 mm.

sample of three eggs was taken after day 14 to determine the events in otolith development.

Sagitta were removed from 10 larvae of each group according to the above schedule and photomicrographed.

LARVAE:

Developing embryos were maintained at 24°C in L12:D12 in hatching jars with running seawater (30‰). Upon hatching, the larvae were di-

vided and subjected to the following conditions:

Group LaD24—Larvae-dark-24 h, constant darkness.
Group LaL24—Larvae-light-24 h, constant light.
Group LaL6:D6—Larvae-light-6 h:dark-6 h.
Group LaL12:D12—Larvae-light-12 h:dark-12 h.

All groups were fed newly hatched brine shrimp ad libitum and kept at 24°C with daily changes of water at 30‰. Samples of 10 larvae from each group were taken at days 0, 6, 9, and 16 except the L12:D12 group, which was sampled daily. Sagitta were removed from each sample and photomicrographed. Scanning electron micrographs were made of samples for comparison with the light micrographs.

RESULTS

Formation of Otoliths in Embryos

The sagittae were the first tissues to calcify and were discernible on days 3 and 4 at embryonic developmental stages 24-28 (Armstrong and Child 1965). An amorphous mass was discernible in the labyrinth region of the larva before calcification was initiated. This mass, the core organic matrix, had a gellike consistency and could be dissected. Calcification was initiated in the core of the sagitta of 30% of the embryos on day 3 and 100% of the cores showed calcification by day 4 (Fig. 3). Increment formation began on day 12, and 20% had one increment. On day 13, 80% had one increment and 20% had two increments. On day 14, the day of hatch, 20% had one increment, 70% had two increments (Fig. 2), and 10% had three increments.

Calcification began with formation of crystals which extended to the edge of the core matrix. Histochemical analyses have shown that calcification begins in the core at the same time that the core becomes birefringent (J. Yamada[6]). Multiple spherules (Fig. 4a, b) are common in the calcified core but their origin and sequence of development is unknown. The newly formed sagittae had a mean diameter of 0.024±0.004 mm. Calcification continued and additional crystals extended beyond the original boundary in an interlocking fashion until the diameter reached 0.048±0.008 mm at day 9 and developmental stage 36. At this time only the core region could be observed, with no increments (Fig. 3). Two days later (on day 11 postfertilization), increment formation was initiated around the core, and the mean sagitta diameter had reached 0.074±0.008 mm. When viewed with transmitted light, the concentric increments consisted of alternate narrow, dark discontinuous zones (D) and wider, lighter, incremental zones (I) (Fig. 3). The D intersected the I at right angles and were concentric with the core and outer surface of the otolith. Upon hatching at day 14, postfertilization, two or three increments were readily discernible as daily increments started forming 2-3 d before hatching.

Otoliths examined with the SEM confirmed the increment counts determined under transmitted light and showed the orientation of the crystals (Fig. 1).

Effect of Light on Increment Formation in Embryos and Larvae

The light cycle to which an embryo or larva was exposed had an effect on increment formation and hatching time. Embryos in the L12:D12 cycle had two or three increments prior to hatching and one increment per day after hatching (Table 1, Fig. 3). Embryos kept in L12:D12 hatched at 14 d while those exposed to other light cycles had longer incubation times and a difference in increment formation during incubation and after hatching was apparent in the other groups (Table 2). Embryos incubated in constant dark (ED24) had a delayed hatch, suppressed increment formation (Fig. 5), and a smaller otolith

TABLE 1.—Sagitta were from *Fundulus heteroclitus* embryos and larvae incubated on a L12:D12 cycle at 24°C (N = 10/d).

Age (days after hatching)	Increment count	Otolith diameter (mm)
0	2.75±0.5	0.128±0.011
1	4.00±0.0	0.150±0.015
2	4.50±0.5	0.158±0.015
3	5.50±0.5	0.180±0.140
4	6.20±1.1	0.187±0.011
5	7.20±1.0	0.203±0.003
6	8.50±1.1	0.220±0.111
7	9.50±0.6	0.240±0.110
8	10.60±0.8	0.255±0.042
9	12.00±1.0	0.268±0.058
10	12.60±0.9	0.280±0.018
15	17.50±1.2	0.350±0.120

[6]Faculty of Fisheries, Hokkaido University, Hakodate, Hokkaido, Japan, pers. commun.

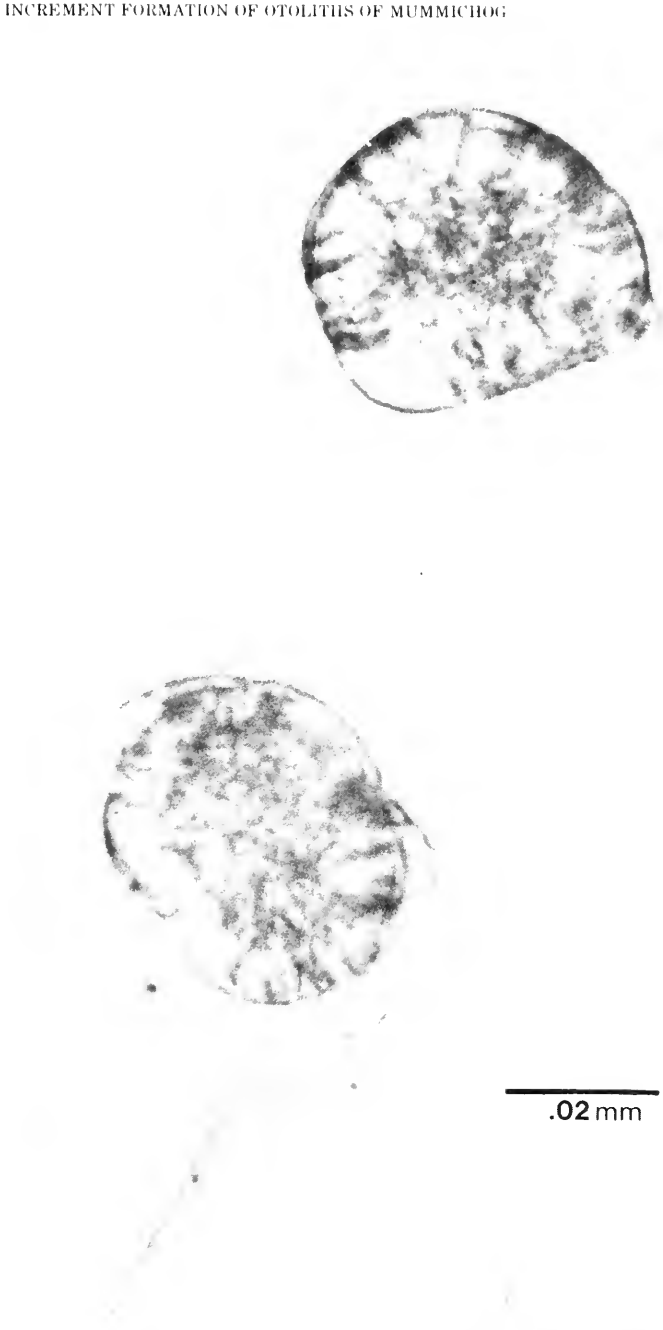

FIGURE 3.—Light micrograph of the core of the sagitta of *Fundulus heteroclitus* taken on day 10 of embryo formation. No increments have yet formed. Bar = 0.02 mm.

diameter (Table 2A, Fig. 5). The embryos incubated in constant light (EL24) hatched at 15 d postfertilization and showed 6.0±0.67 increments when sampled 3 d after hatching (Table 2B). Constant light conditions did not significantly alter increment formation; the constant light group (EL24) showed the same number of increments as in the EL12:D12 group at 3 d of age. Thus, the effect of light on embryonic increment formation and otolith diameters was the same for the EL24 and EL12:D12 groups.

A 1-min light stimulus on day 10 of ED24+L

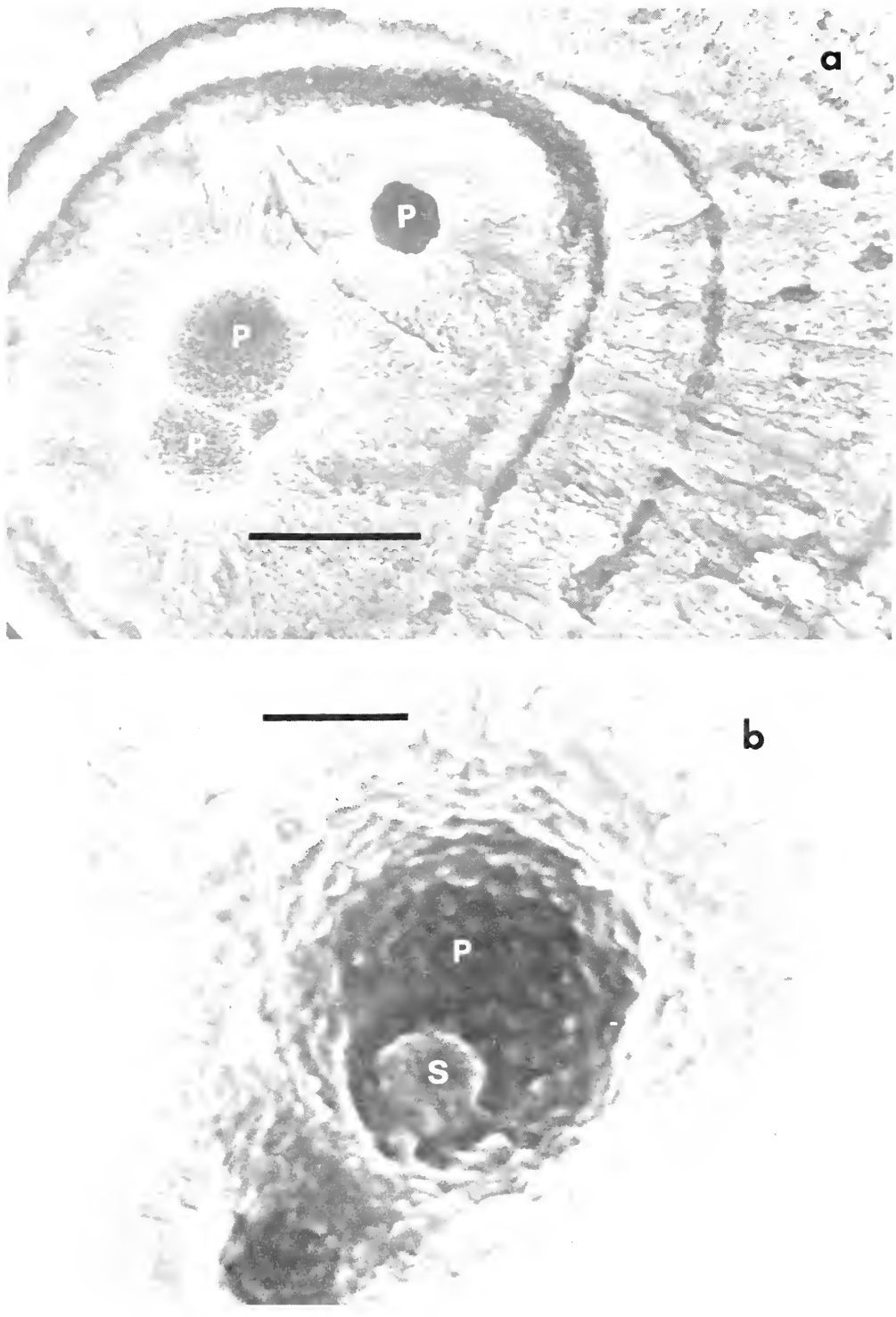

FIGURE 4.—a) SEM of the core of the sagitta of *Fundulus heteroclitus* showing the core (C) and the multiple primordia (P) surrounds the spherules. Bar = 1 μ. b) SEM showing a spherule (S) in the multiple primordia (P) of the core (C) or the sagitta. B = 0.5 μ.

resulted in increment formation (Table 2C) in embryos otherwise maintained in constant darkness. Increment counts for ED24+L were less than those of the EL24 group and the EL12:D12 group at 3 d after hatching, but were very close to the increment counts found at day 2 of the EL12:D12 group.

TABLE 2.—Effect of photoperiod and light stimuli on increment formation in sagittal otoliths of *Fundulus heteroclitus* embryos.

A) Embryos were incubated in total darkness and sagitta were removed 3 d after hatching (ED24)
B) Embryos were incubated in constant light and sagitta were removed 3 d after hatching (EL24)
C) Embryos were incubated in constant darkness with 1 min of light at day 10 of development. Sagitta were removed 3 d after hatching. N = 10 in all groups. (ED24+L)

	Sagitta diameter (mm) ($\bar{X}\pm$SD)	Increment numbers ($\bar{X}\pm$SD)
A	0.071±0.008	0.6±0.77
B	0.177±0.013	6.0±0.67
C	0.146±0.012	4.7±0.48

The effect of light on larvae which were maintained under EL12:D12 during embryonic development and then transferred to constant darkness after hatching was not as evident as the effect of light was in the embryos maintained in constant darkness. Larvae raised in constant darkness (LaD24) showed a rapid addition of increments between day 0 and day 6 after hatching, but few increments formed after day 6 (Table 3). When the LaD24 data were compared with the data from the larvae hatched and raised

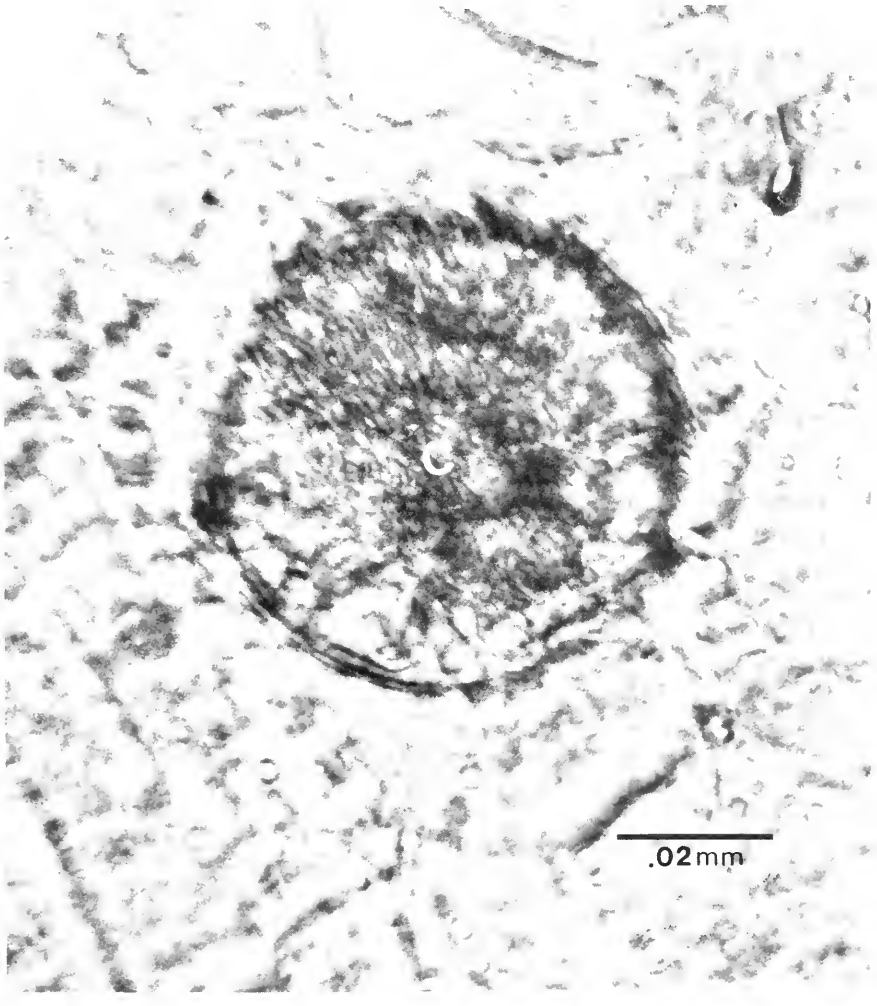

FIGURE 5.—Light micrograph of the sagitta from a newly hatched larvae incubated for the total embryonic period in total darkness. Core formation is present but no increments have formed. Bar = 0.02 mm.

TABLE 3.—Otoliths are from *Fundulus heteroclitus* larvae. Embryos were incubated on a L12:D12 cycle and the larvae transferred to constant darkness at 24°C immediately after hatching.

Age	Increment count	Otolith diameter (mm)
0	2.75±0.5	0.128±0.011
6	13.89±1.69	0.181±0.010
9	15.22±0.83	0.190±0.010
16	15.60±2.01	0.204±0.015

in EL12:D12 (Table 1), sagitta of LaD24 had reduced increment numbers after day 6 and sagitta diameters in experimental fish were smaller than those found in the control (LaL12:D12).

Some groups that had increment formation (LaD24 and LaL6:D6) during the first 6 d had increments formed after day 6 that were unclear and it was difficult to differentiate the D and I in the outer areas. However, the LaL12:D12 group showed distinct increments beyond day 6.

The ED24 group larvae were sluggish upon hatching as were the ED24±L group. The larvae appeared to be normal in every other fashion except that the yolk sacs were notably smaller than the 12L:12D group.

Effect of Temperature and Body Growth on Otolith Formation in Larvae

An increase in temperature caused an increase in the growth rate in the larvae (Fig. 6a). The 30°C group grew significantly faster than the 24°C group ($P<0.05$).

The 30°C larvae, also formed otoliths (Fig. 6b) which were significantly larger ($P<0.05$) in diameters than those in fish held at 24°C. However, the difference in growth rates had no effect on the increment counts from either group (Fig. 6c). Both showed daily increment formation in their otoliths but the faster growing otoliths had wider daily increments, which accounted for the increased diameter measurements. When the otolith diameter data were pooled and compared with length data, the relationship was highly correlated ($r = 0.95$; Fig. 7).

Estimation of Age of Wild Fish

It is difficult to gain any insight into the age structure of the wild population from the length-frequency histograms, e.g., larvae collected 9 June 1977 had a standard length-frequency

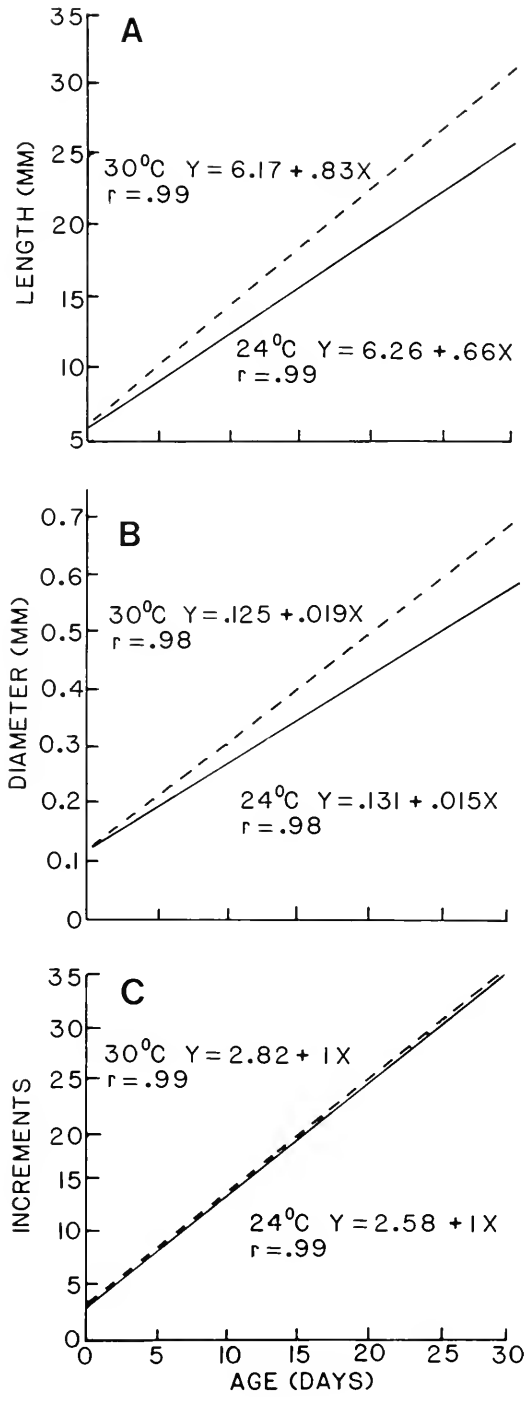

FIGURE 6.—A regression plot of A) standard length (SL), B) the diameter of the sagitta, and C) the numbers of increments of the sagitta of *Fundulus heteroclitus* reared at 24°C and 30°C plotted against age of the fish.

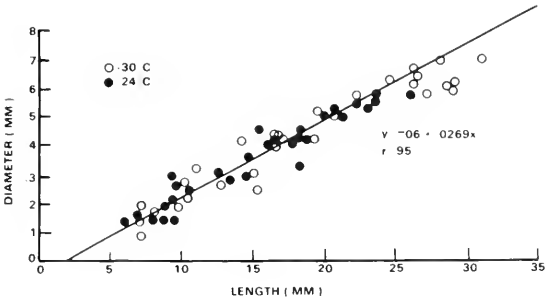

FIGURE 7.—A regression plot of the diameters of all of the 24° and 30° *Fundulus heteroclitus* sagitta plotted against the standard length of the fish.

mode of 23 mm (Fig. 8a). However, otolith increment-frequency histograms of the sample enabled us to differentiate cohorts (Fig. 8b).

A statistical analysis of the data from the field population showed that the relationship between the length of the fish and otolith diameter was linear ($y = 0.01 + 0.027x$, $r = 0.90$). The relationship of increment number and otolith diameter was curvilinear ($y = 0.7601 - 0.0217x + 0.000rx^2$, $r = 0.92$). Thus, the diameter of the otolith increased as the fish grew; the width of the increment was wider in younger, smaller fish than in older, larger fish; and the number of increments increased as the length of the fish increased.

When the time of hatching was estimated, using increment counts (Fig. 9a), groups were found that correlated with the occurrence of new and full moons. We observed that the increments tended to be more distinct in larvae collected from the field than in laboratory-reared larvae. When ages were adjusted for the two or three prehatching increments, the relationship was even more obvious (Fig. 9b). Incremental data indicated that the fish collected hatched at the new and full moon spring tides.

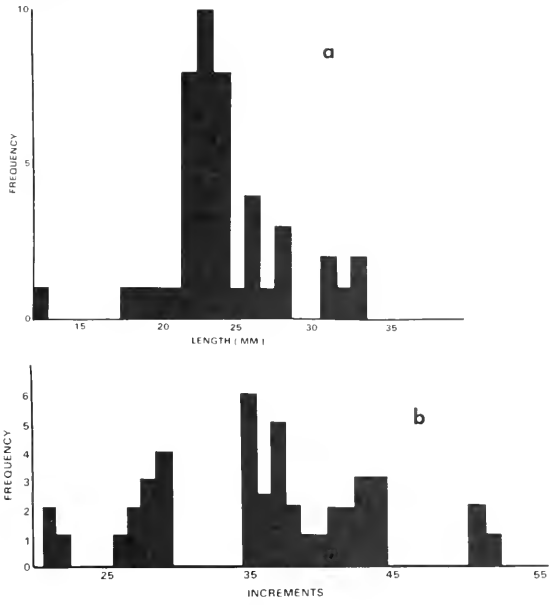

FIGURE 8.—a) A length-frequency histogram of all fish collected in the sample. b) A histogram showing the frequency of the increment number of the sagitta of same fish as in 8a.

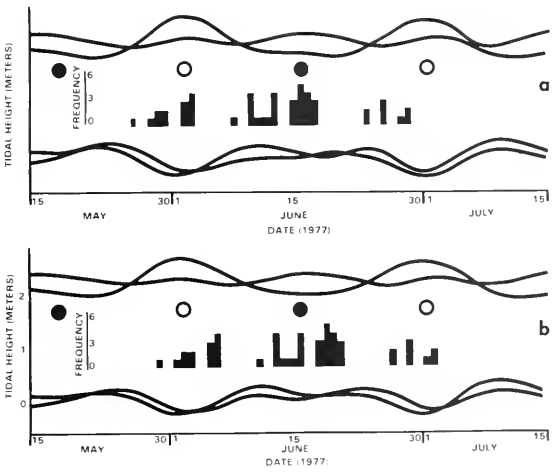

FIGURE 9.—*Fundulus heteroclitus* larvae collected on 9 June 1977. a) Estimated hatching dates are determined from numbers of increments in the sagitta; b) estimated hatching times are adjusted for the two increments formed prior to hatching. Also represented are diurnal high tides (upper lines) and low tides (lower lines) and lunar phase (open circles = full moon, closed circles = new moon).

DISCUSSION

Embryological Formation of Otoliths

Otoliths (sagittae) are the first calcified tissues to form in developing *F. heteroclitus* embryos, and although they are prominent and easily observed features that have been presented in numerous developmental studies, their formation is not discussed. Long and Ballard (1976) clearly showed otoliths that formed at stage 20 in embryos of the white sucker, and Armstrong and Child (1965) showed otoliths in mummichog embryos at stage 23 with calcification at stage 24,

which agreed with this study, but their ontogeny is not well known. The importance and functional nature of the early otolith calcification has not yet been determined.

Two or three increments were easily visible in the mummichog otolith at the time of hatching. Accurate age determination of field samples could be affected until the number of increments formed at the time of hatching is considered. Brothers et al. (1976) studied increment formation in several fish species and found that the California grunion, *Leuresthes tenuis*, had two increments at hatching. Some species, such as the northern anchovy, *Engraulis mordax*, had no increment formation until the time of yolk-sac absorption, 6 d after hatching (Methot and Kramer 1979). Taubert and Coble (1977) found that three species of *Lepomis* began increment formation at swim up. Scott (1973) studied the otolith structure in larvae of the northern sand lance, *Ammodytes dubius*, and suggested that otoliths first formed in the postlarvae at a mean total length of 2.4 cm. However, his interpretation was a result of back calculations, not direct observations of otoliths from known age or larval stages of the fish.

We have found that multiple spherules in the core of the sagitta, followed by numerous increments, are formed prior to hatching in the Asiatic salmon or masou, *Oncorhynchus masou*; chum salmon, *O. keta;* pink salmon, *O. gorbuscha*; Arctic char, *Salvelinus alpinus*; brook trout, *S. fontinalis*; rainbow trout, *Salmo gairdneri*; and the sculpin, *Cottus nozawa*. The juveniles of the live bearing guppy, *Lebistes reticulatus*, and mosquitofish, *Gambusia affinis*, form a large number of increments prior to being spawned (Radtke and Dean unpubl. data). Mummichogs, California grunion, and the Atlantic silverside, *Menidia menidia*, have tidally correlated incubation periods of about 10 to 14 d and the salmonids incubation period can exceed 50 d. In contrast, the northern anchovy and spot, *Leiostomus xanthurus*, have short incubation periods of <2 d. This indicates that embryos which have longer incubation periods and large yolk sacs may form several increments before hatching, while embryos that have short incubation periods might not start increment formation until hatching or after yolk-sac absorption (Brothers et al. 1976; Methot and Kramer 1979). Much work remains to be done on a range of species before we can attempt to interpret the functional significance of increment formation in embryos.

The Effect of Light on Increment Formation in Embryos and Larvae

The increments observed in otoliths in this and other studies (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977; Barkman 1978; Methot and Kramer 1979) appear to be indicators of daily biological events. Rhythmic physiological activities, such as the occurrence of rhythmic mineral deposition in coral (Wells 1963), crayfish gastroliths (Scudamore 1947), and marine bivalves (Clark 1968; Pannella and MacClintock 1968), are controlled to a large extent by environmental changes synchronized to the diurnal astronomical cycle.

The only examination of the effect of endogenous daily biological rhythms on fish otoliths was by Taubert and Coble (1977), who studied the effect of environmental factors on daily increment formation of *Tilapia mossambica* larvae hatched in constant light. Their different experimental groups all showed increment formation but it was not always daily. They found normal increment formation in all experimental groups with a 24-h periodicity and any other cycle other than 24-h period disrupted increment formation. Since daily cycles are known to occur in blood chemistry of fish (Garcia and Meier 1973), those daily chemical changes could be reflected in the daily increments of the otoliths. Mugiya (1966) found monthly changes in total and diffusible calcium in the endolymph of the semicircular canals of the rainbow trout and the flatfish, *Kareius bicolaratus*, and he related his finding to the formation of the opaque and translucent zones found in adult otoliths. Daily changes in the calcium metabolism of the fish also occur (Mugiya et al. 1980) which are reflected in the formation of the I and D.

Daily increments were formed in *F. heteroelitus* larvae kept in a L12:D12 cycle, but were absent when the developing embryos were kept in constant darkness (Fig. 5). Light had a definite effect on increment formation, as embryos kept in constant light showed increment formation and otolith diameters that were comparable with the L12:D12 group. An insight into this discrepancy was gained in the analysis of the group which initiated increment formation after a light stimulus on day 10 after fertilization. The possibility that light is a synchronizing stimulus at the cellular level was demonstrated by Pitten-

drigh and Bruce (1957), who showed that a light stimulus synchronized emergence in fruit flies. More study is necessary to determine the timing of light needed for increment formation as well as the quantity and quality of light necessary. Whether the control of increment formation is an endogenous or exogenous rhythm (Harker 1957) is beyond the scope of these experiments. But the experiment on increment initiation in the dark group with 1 min of light exposure on day 10 indicated that light can act as a synchronizing stimulus, similar to that observed by Pittendrigh and Bruce (1957). Mugiya et al. (1980) found that D formation was initiated when light interrupted a photo period of 12L:12D or longer light period, but they did not determine the minimum dark period necessary for formation of the D or the free running period for the D and I.

When *F. heteroclitus* larvae were hatched in L12:D12 and then placed in light regimes other than a 24-h photoperiod, the increment formation became aphasic in each group and increment formation occurred at a slower rate. The "biological clock" of this group seemed to be out of phase under photoperiods other than those with a 24-h periodicity. A great deal of very exciting work is necessary to resolve these fundamental questions on increment control.

Effects of Temperature and Body Growth on Otolith Formation in Larvae

Under the various experimental conditions employed in this study, daily otolith increments formed regardless of body growth or otolith growth rate (Fig. 6a, b, c), so it was possible to determine age and daily growth rates of individual larvae which lived under different environmental conditions. Although *F. heteroclitus* larvae grew faster at 30°C than at 24°C, the number of increments was still directly related to chronological age. This documents the reliability of otolith increments for the age estimation of mummichog larvae. It has been demonstrated that daily increments exist in several other species of fish (Pannella 1971, 1974; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Ralston 1976; Taubert and Coble 1977) and the relationship between increment counts and fish and otolith size was shown for the Atlantic silversides (Barkman 1978). In this study, otolith diameter increased with increased body length and increments formed on a daily basis with wider increments found in younger fish than older fish. This is consistent with the fact that younger fish are growing faster, and although the relationship is nonlinear, it is predictable and these results are consistent with those of Methot and Kramer (1979).

Estimation of Age of Wild Fish

Daily increments observed in field samples were easier to interpret than increments found in laboratory-reared larvae. We were not able to make age estimations of field collections of mummichogs from length-frequency histograms, but it was possible to determine the age and growth rate of individual larvae from increment counts.

Ralston (1976) and Struhsaker and Uchiyama (1976) determined growth rates of the millet-seed butterfly fish, *Chaetodon miliaris*, and the nehu, *Stolephorus purpureus*, respectively, and found that the growth, as represented in incremental units in the otolith, was nearly linear. Similar results were obtained by Barkman (1978) for Atlantic silversides and Methot and Kramer (1979). Our results are consistent with theirs: that increment formation is independent of growth rate but is age dependent; thus growth rates can be estimated for individual larval fish.

Analysis of the age structure of samples of wild larval mummichogs showed that larvae hatched on or near the time of full and new moons. This is corroborated by observations on the reproductive biology of *F. heteroclitus* by Taylor et al. (1977, 1979) and DiMichele and Taylor (1978), New Zealand white bait, *Galaxias maculatus*, by McDowell (1968), and Atlantic silversides by Middaugh (1981). Eggs of the California grunion, an intertidal spawner, have been found to hatch during spring tides (Clark 1925) and have otolith increments at hatching (Brothers et al. 1976). An analysis of age structure of wild populations of mummichog larvae, as determined from their otoliths showed that South Carolina mummichogs spawn from March to mid-August and have a lunar spawning periodicity during that season. Analysis of otolith increments enabled us to differentiate individual fish in the wild population of the same size but of different ages.

Photoperiod is a critical factor in increment formation, but other factors such as diurnal migratory behavior, rhythmic feeding, temperature, respiration, and tidal rhythms might also

play significant roles. Even though the control and/or mechanism of daily increment formation in larval fish is not fully understood, the increments are a powerful tool for analysis of individual growth and age determination of very young fish.

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THE LARVAL DEVELOPMENT OF *SERGESTES SIMILIS* HANSEN (CRUSTACEA, DECAPODA, SERGESTIDAE) REARED IN THE LABORATORY

MARGARET KNIGHT[1] AND MAKOTO OMORI[2]

ABSTRACT

The larval development of *Sergestes similis* Hansen reared in the laboratory includes the following stages: nauplius I-IV, protozoea I-III, and zoea I-II. These forms together with the first two postlarval stages are described and illustrated.

Sergestes similis and *S. arcticus*, closely related species which comprise the *arcticus* species group, are very similar in larval as well as adult morphology especially in the ornate armature of protozoeal carapace apparently specific to the group. In contrast, the two species of the *atlanticus* group, *S. atlanticus* and *S. cornutus*, differ distinctly from each other in carapace armature of the protozoeal stages. The difference between these two species groups in variation within each group indicates that larval morphology may be of value in the study of interspecific relationships within *Sergestes*. *Sergestes similis* and *Sergia lucens*, species of closely related genera, differ in number of naupliar stages, in armature of body in protozoeal and zoeal phases, and in development of some appendages.

The pelagic shrimp *Sergestes similis* is abundant in the North Pacific Drift ranging from Japan to North America between 40° and 50°N, and is a prominent constituent of the plankton in the cooler waters of the California Current.

Within the genus *Sergestes* (Omori 1974), *S. similis* is located in the *arcticus* species group, as defined by Yaldwyn (1957), which includes only the two species *S. arcticus* Kröyer and *S. similis* Hansen. *Sergestes arcticus* is widely distributed, occurring in the North Atlantic, the Mediterranean, and all sectors of the Southern Ocean, while *S. similis* is restricted to the subarctic and transitional zones of the North Pacific; available data indicates that the species are geographically isolated from one another (Judkins 1972). The life history and distribution of *S. similis* and its importance in oceanic ecosystems of the Pacific have been discussed by Pearcy and Forss (1969), Omori et al. (1972), and Omori and Gluck (1979).

The purpose of this paper is to describe and illustrate the larval development of *S. similis* and to compare the larvae with those of the closely related species *S. arcticus* described by Wasserloos (1908), Hansen (1922), and Gurney and Lebour (1940). The larvae of *S. similis* are also compared with the early stages of *S. atlanticus* and *S. cornutus* (Gurney and Lebour 1940), which comprise the *atlanticus* group, to note the difference in variation within species groups in protozoeal morphology, and with the larvae of *Sergia lucens* (Omori 1969) to note the differences between species of closely related genera. The description of *Sergestes similis* is based on both individuals reared in the laboratory by Omori (1979) during his study of the growth, feeding, and mortality of larval and postlarval stages of the species off southern California, and on specimens from preserved plankton samples.

Gurney and Lebour (1940), in the major work on larvae of the genus, remarked that "perhaps the most interesting feature of the development of *Sergestes* is the striking difference which exists between the larvae of the different species, while the adults are often separable with difficulty," and suggested that knowledge of the larvae, when complete, may give a better indication of the relationships of species than adult morphology.

METHODS

Omori (1979) described the procedures used for rearing the larvae of *S. similis* in the laboratory. Larvae from the population of the

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species off the coast of southern California were obtained for study from preserved plankton samples taken on Scripps Institution of Oceanography Expedition X and CalCOFI Cruises 6904 and 6905 during April and May of 1964 and 1965.

At least five individuals of each developmental stage were dissected in glycerine for study of appendages. Some specimens of each stage were prepared for study and dissection by digesting away all soft tissue in heated aqueous KOH and then staining with Chlorazol Black E. Drawings were prepared with the drawing attachment of a Wild M20[3] microscope.

Measurements of reared and planktonic larvae of *S. similis* were compared by Omori (1979, table 6); the mean body lengths (with standard deviation in parentheses) of larval stages obtained at 14°C are repeated here by stage for convenience. The larvae were measured along the midline from anterior margin of forehead to posterior margin of telson.

The postnaupliar developmental phases have been named protozoea, zoea, and postlarva following Omori (1979), and the terminology of Gurney and Lebour (1940) has been followed in describing the armature of carapace. In the protozoeal phase the outgrowths of the carapace are referred to as processes with secondary spines and spinules, while in the zoeal and postlarval stages the outgrowths are called spines with secondary spinules.

Segmentation of two of the appendages proved difficult to determine. The basal segmentation of the exopod of the second antenna in protozoeal stages I-III was not clear. In *S. similis* it appeared that there were incomplete sutures within segments 1 and 3, giving 12 outer margin and 10 inner margin sutures; we have numbered the segments along the inner margin. The articulation of coxa, basis, and endopod of the second maxilla in protozoeal and zoeal phases also proved confusing. We have followed Gurney (1942) in referring to the medial lobes as bifid endites of coxa and basis, and have assumed from the morphology of the postlarval appendage that the endopod consists of 5 segments, although the articulation of segment 1 and basis was not clear.

In the description of larval stages, only changes in structure and armature of body and appendages are discussed; if an appendage is not mentioned, it may be assumed that there has been no change from the preceding stage except increase in size.

In order to compare the basic pattern of development between *Sergestes similis* and *Sergia lucens*, we reexamined a number of larvae and postlarvae of *S. lucens* from the rearing experiment in July 1965.

RESULTS

The larval development of *Sergestes similis* includes the following stages: nauplius I-IV, protozoea I-III, and zoea I-II. The first two postlarval stages are also described.

Nauplius I (Fig. 1a, e)

Body length: 0.34 mm (0.01).

Body ovoid with two posterior spines which curve posterodorsally and are slightly swollen basally.

Antennule (Fig. 2a) unsegmented with 4 smooth setae, 2 terminal and 2 subterminal, and small terminal spine.

Antenna (Fig. 3a) unsegmented; exopod with 5 setae; endopod with 3 setae, 2 terminal and 1 subterminal; all setae smooth.

Mandible (Fig. 4a) biramous and unsegmented, each ramus with 3 smooth setae.

Nauplius II (Fig. 1b)

Body length: 0.38 mm (0.01).

Body slightly longer and narrower posteriorly than in stage I, with 2 pairs of spines on posterior margin, outer pair very short, tiny rudiments of third inner pair sometimes visible.

Antennule (Fig. 2b) with 1 subterminal medioventral seta and 3 terminal processes including 2 setae with setules and 1 small aesthetasc.

Antenna (Fig. 3b) unsegmented; exopod with 6 setae and sometimes with small distal spine, distolateral seta smooth and others plumose; endopod with 2 plumose setae and 1 small spine terminally.

Mandible (Fig. 4b) with 3 plumose setae on each ramus.

Nauplius III (Fig. 1c, f)

Body length: 0.42 mm (0.02).

Body with posterior portion tapering, posterior margin slightly indented medially with 4

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

FIGURE 1.—*Sergestes similis*. Nauplius I-IV, a-d, dorsal view; nauplius I, III-IV, e-g, lateral view without appendages.

pairs of spines, outer pair tiny, relatively long third pair armed with spinules and articulated basally.

Antennule (Fig. 2c) sometimes with a second seta on inner margin, incipient segmentation, and few rows of tiny spinules.

Antenna (Fig. 3c) with incipient segmentation of protopod and exopod sometimes visible; exopod with 7 setae and small distal spine, distal 2 setae with small setules, other setae plumose; endopod with 3 terminal setae and 1 seta on inner margin.

FIGURE 2.—*Sergestes similis*. Antennules: a-d, nauplius I-IV; e-g, protozoea I-III; h-i, zoea I-II; j, postlarva I; setules omitted on i and j.

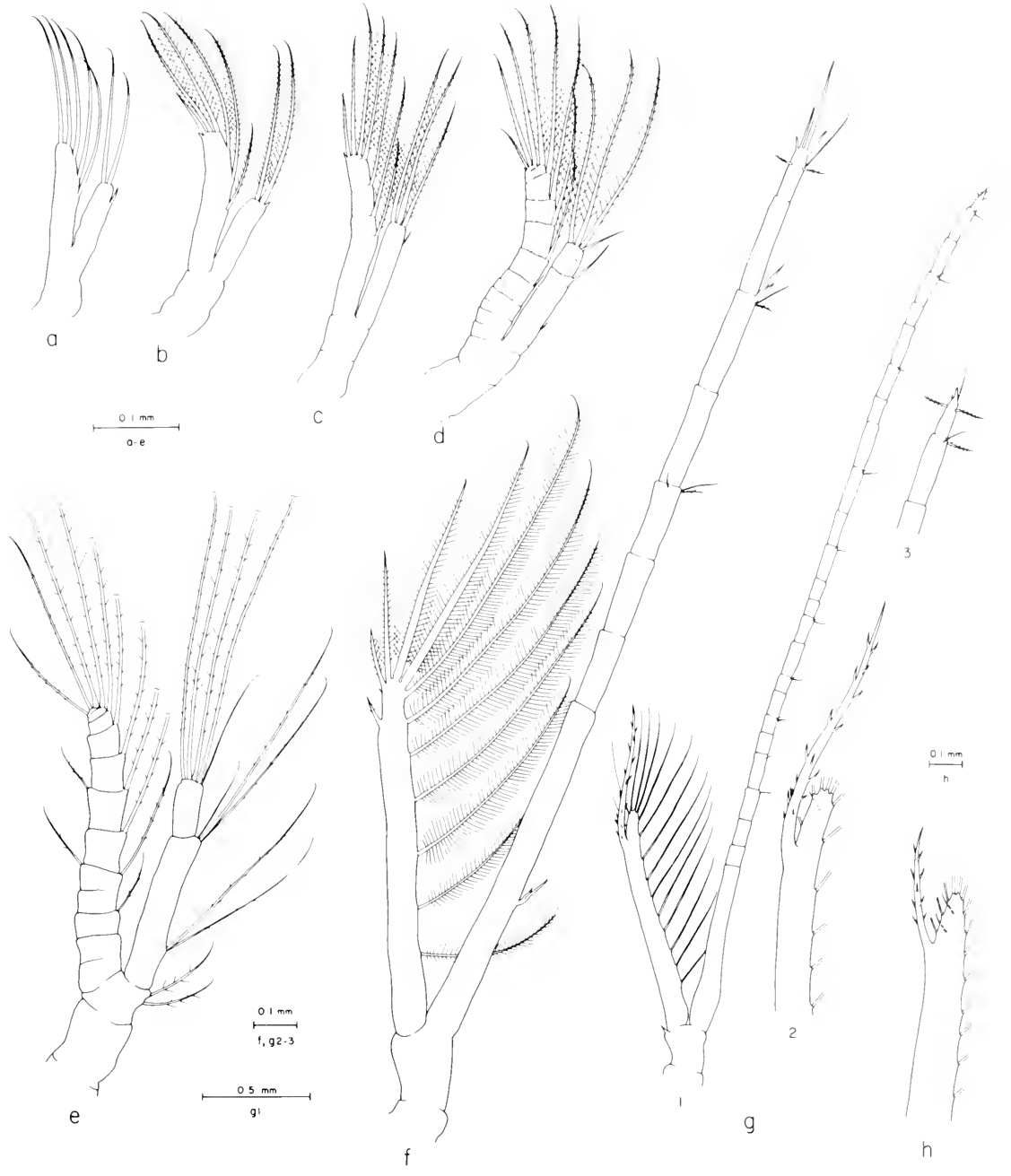

FIGURE 3.—*Sergestes similis*. Antenna: a-d, nauplius I-IV; e, protozoea I; f-g, zoea I-II; h, postlarva I, tip of scale; setules omitted on g.

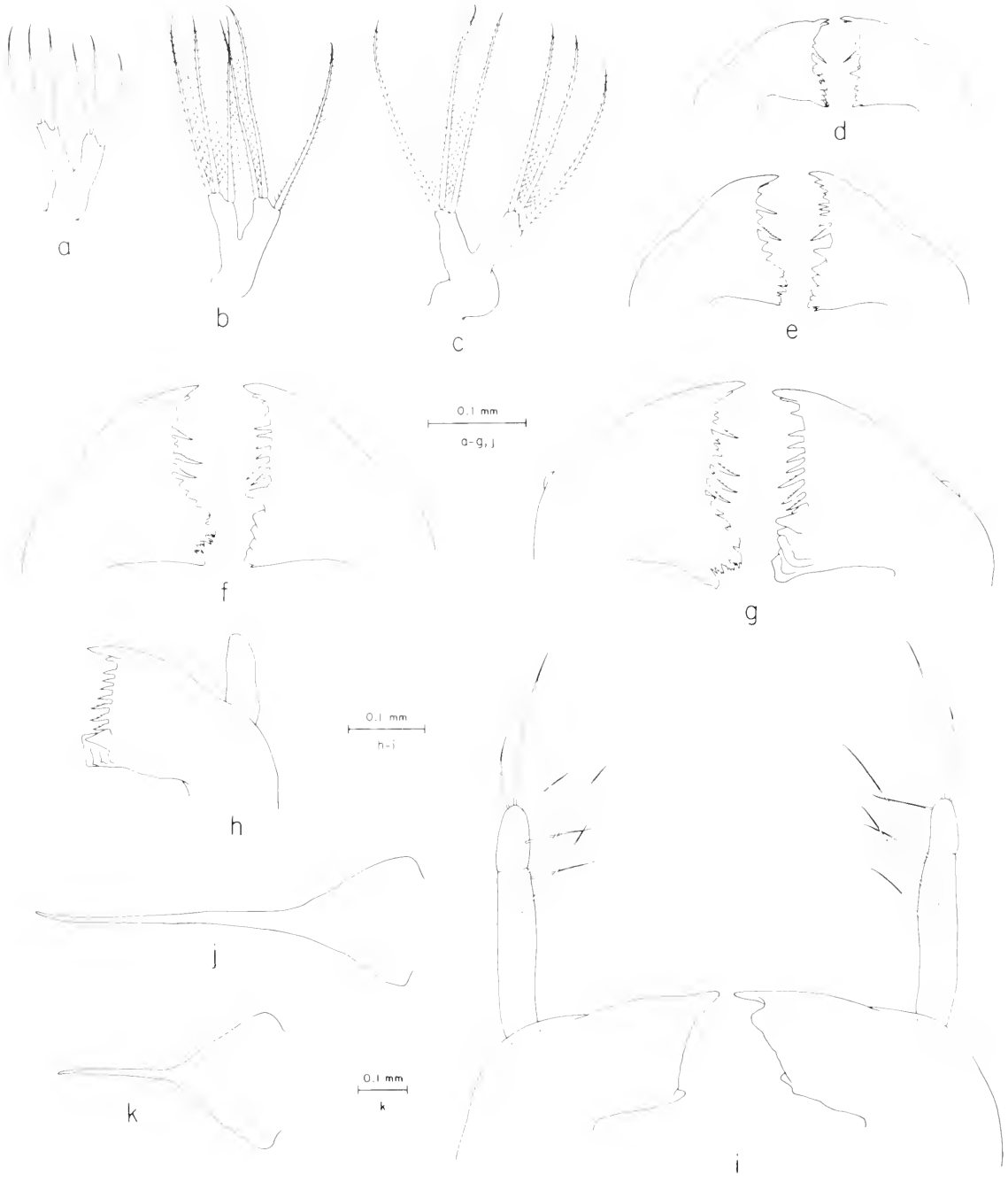

FIGURE 4.—*Sergestes similis*. Mandibles: a-e, nauplius I-II, IV; d-f, protozoea I-III; g-h, zoea I-II; i, postlarva I. Labrum: j, protozoea I; k, zoea I.

Mandible unchanged.

Anlagen of maxillules, maxillae, and first and second maxillipeds visible.

Nauplius IV (Fig. 1d, g)

Body length: 0.49 mm (0.03).

Body with abdomen forming, posterior margin with distinct medial indentation and 4 pairs spines, third pair still relatively long, rudiments of fifth inner pair sometimes visible, spinules present on spines 2-4, and sometimes on 1; third pair articulated, other spines fused with telson.

Antennule (Fig. 2d) with 2 inner setae, terminal setation unchanged; proximal two-thirds with indistinct segmentation most clearly visible along inner margin; about 17 rows of tiny spinules encircle antennule associated, in segmented section, with distal margin of segment.

Antenna (Fig. 3d) with protopod of 2 indistinct segments; exopod with approximately 8 segments (basal segmentation unclear, specimens cleared and stained have indication of 10 segments on outer margin and about 8 on inner margin), with 8 or 9 setae and sometimes a small distal spine, distal 3 setae with small setules, others plumose; endopod at least 2-segmented, small distinct distal segment with 4 terminal setae, proximal segment with 2 setae on outer margin and sometimes with incomplete basal segmentation; both rami encircled with rows of tiny spinules.

Mandible (Fig. 4c) with basal portion swelling with development of gnathal lobe, tissue withdrawing from rami.

Rudiments of maxillules, maxillae, and 2 pairs of maxillipeds present posterior to mandibles.

Protozoea I (Fig. 5a, b)

Body length: 0.82 mm (0.02).

Carapace with following processes: 1 pair anterolateral, each branching to 3 large spines and occasionally 1-3 small spines (5 of 20 reared larvae with small spines on one or both processes, 20 larvae from the plankton with 3 large spines only); 1 pair lateral with 1-3 large basal spinules; 1 posterodorsal with few large basal spinules, usually 2; all processes with small spinules to tip. Anterior margin of forehead with pair of small papillae. Prominent, round dorsal organ present in protozoeal phase. Thorax with evidence of segmentation, abdomen unsegmented. Telson forked, each fork with 2 small smooth ventral spines and 4 long curving processes armed with spinules.

Antennule (Fig. 2e) of 3 segments, proximal segment subdivided into 5 small segments; proximal and middle segments with 1 and 2 setae, distal segment with 8 processes including 5 setae, 3 terminal and 2 proximal, and 3 aesthetascs. Gurney (1942) noted that distal segment with aesthetascs is homologous with outer flagellum of later stages and that peduncle is therefore of 2 segments.

Antenna (Fig. 3e) with exopod of 10 segments, terminal segment with 3 setae, segments 2-9 with 1 distal seta on inner margin, segments 3 and 5 with 1 distal seta on outer margin as well; endopod 2-segmented, distal segment with 5 terminal setae, long proximal segment with 5 setae on inner margin—3 distal and 2 proximal on slight protuberance; basis with 2 setae on inner margin; structure unchanged in protozoeal phase.

Mandibles (Fig. 4d) without palp, gnathal lobe of each mandible with 1 strong serrated spine on cutting edge between incisor teeth and molar area. Labrum (Fig. 4j) with long anteroventral spine in protozoeal phase.

Maxillule (Fig. 6a) with exopod a small round lobe bearing 4 plumose setae; endopod 3-segmented with 3-2-5 setae progressing distally; basal and coxal endites with 4 and 5 setae, respectively.

Maxilla (Fig. 7a) with segmentation indistinct; exopod small and oblong with 5 long plumose setae; endopod 5-segmented with setation of 4-2-2-2-3, segment 1 rarely with 3 setae; basal and coxal endites bifid, the 4 median lobes with 8-4-4-4 setae.

First maxilliped (Fig. 8a) with exopod of 1 segment bearing 7 long plumose marginal setae; endopod 4-segmented with 3-2-2-5 setae; basis with 12 setae in groups of 3 along medial margin; coxa with 5 setae; inner margins with fine setules as well.

Second maxilliped (Fig. 9a) with exopod of 1 segment bearing 6 marginal plumose setae; endopod 4-segmented with 2-1-2-5 setae; basis with 5 and coxa with 2 setae.

Third maxilliped a small bud.

Protozoea II (Fig. 10a, b)

Body length: 1.21 mm (0.10).

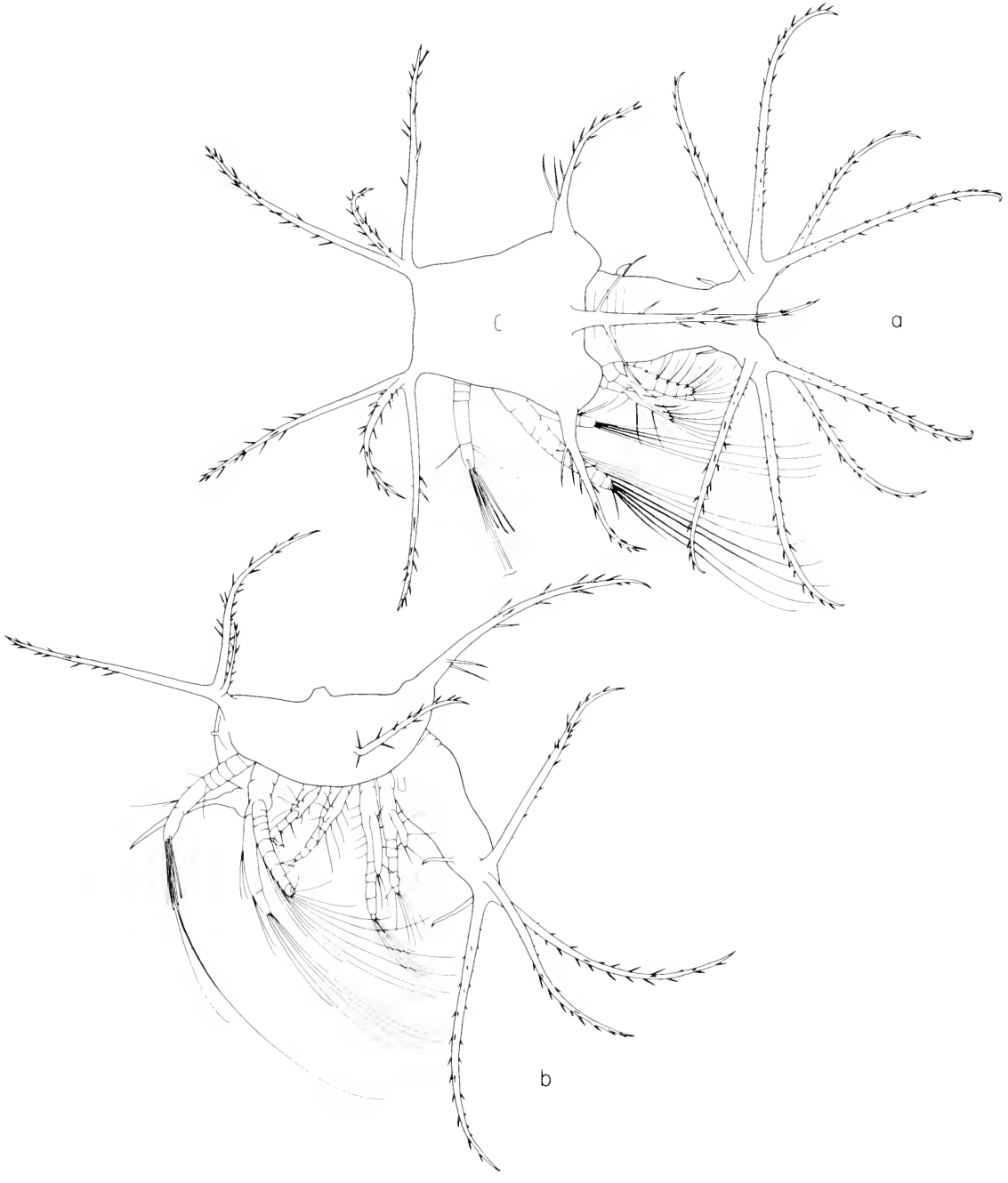

FIGURE 5.—*Sergestes similis*. Protozoea I: a, dorsal view; b, lateral view.

Carapace with rostrum but without pair of anterolateral processes; all processes with relatively large spines which branch distally into several small spinules, the processes themselves do not branch distally but bear small spinules to tip; rostral process with 3 pairs of spines, each lateral process usually with 7, rarely 6 or 8, spines, and posterior process with 2-4, usually 3 or 4, pairs of spines. Eyes stalked and moveable with papilla on anterior margin of stalk. Thorax

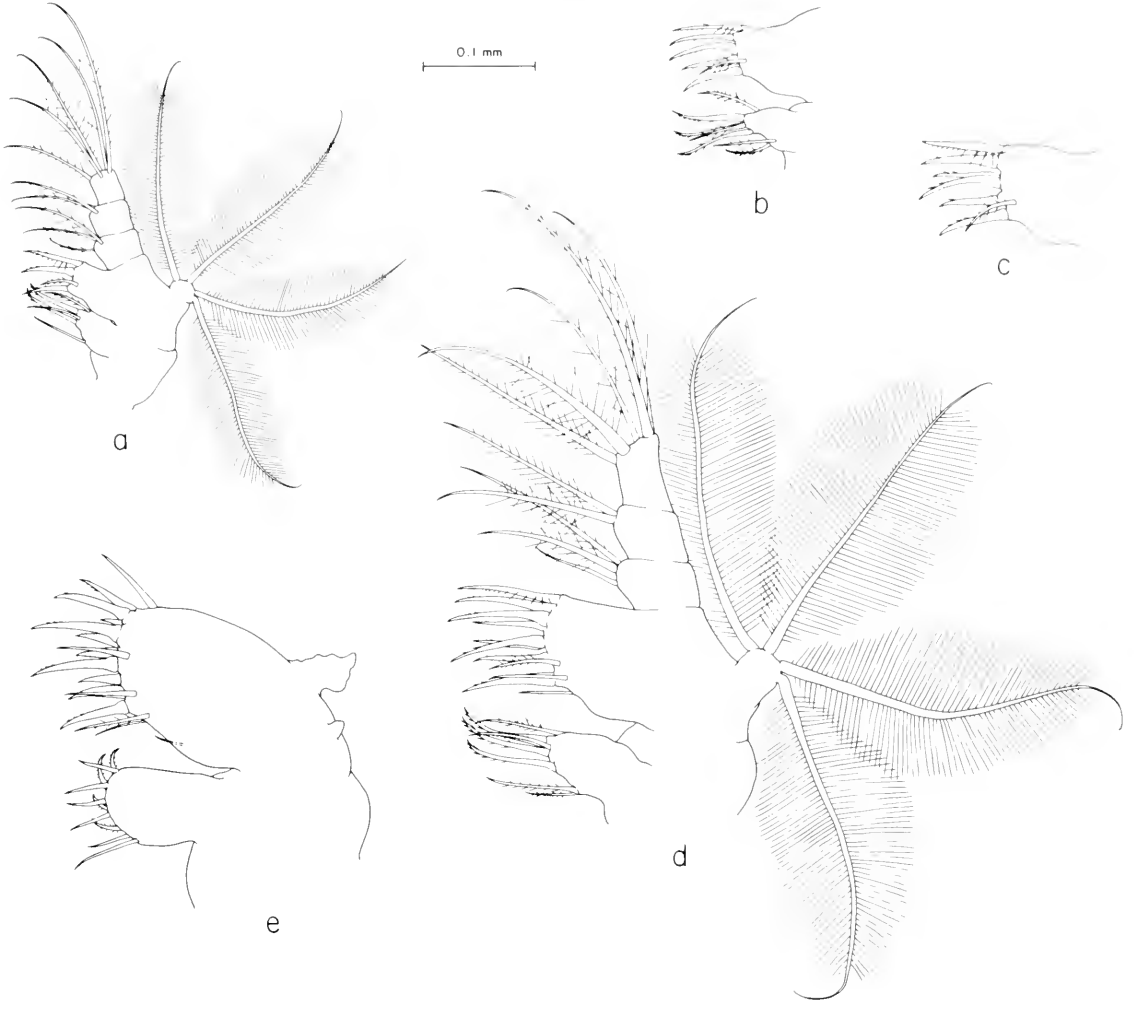

FIGURE 6.—*Sergestes similis*. Maxillule: a, protozoea I; b, protozoea II, coxal and basal endites; c, protozoea III, basal endite; d, zoea I; e, postlarva I.

with segments delineated; abdomen and telson as in preceding stage.

Antennule (Fig. 2f) with 4 subdivisions of proximal segment and distal segment with 9 processes, including 5 setae and 4 aesthetascs.

Mandibles (Fig. 4e) with median armature asymmetrical, right mandible with 2 and left mandible with 5 strong spines, the spine nearest molar area is strongest on each mandible, 2 long spines on right mandible separated by short tooth.

Maxillule (Fig. 6b) with 6 setae on basal endite and 6 or 7, usually 7, setae on coxal endite.

Maxilla (Fig. 7b) with setation of 8-4-5-5 on medial lobes.

First maxilliped with 7 or 8, usually 8, setae on coxa.

Second maxilliped with endopod setation of 2-2-2-5; basis with 5 or 6, rarely 6, setae.

Third maxilliped a small rudiment, sometimes slightly bifid at tip.

Anlagen of thoracic legs 1-5 may be visible.

Protozoea III (Fig. 11a, b)

Body length: 1.90 mm (0.18).

Carapace with 1 pair supraorbital processes which curve dorsolaterally in addition to armature of preceding stage; all processes but rostrum armed with strong spines which branch

FIGURE 7.—*Sergestes similis*. Maxilla: a, protozoea I; b, protozoea II, basal endite; c, zoea I; d, postlarva I.

distally into spinules, all processes terminate in single spine and bear spinules to tip; supraorbital processes each with 9-14, usually 10-12, spines; each lateral process with 5-8, usually 7, spines; and posterodorsal process with 7-13, usually 10-12, spines. Eyestalks longer than in stage II. Abdomen with 5 segments articulated, segment 6 still fused with telson; segments 1-5 with 1 pair lateral spines, segment 6 with biramous, unsegmented, nonsetose uropods and 1

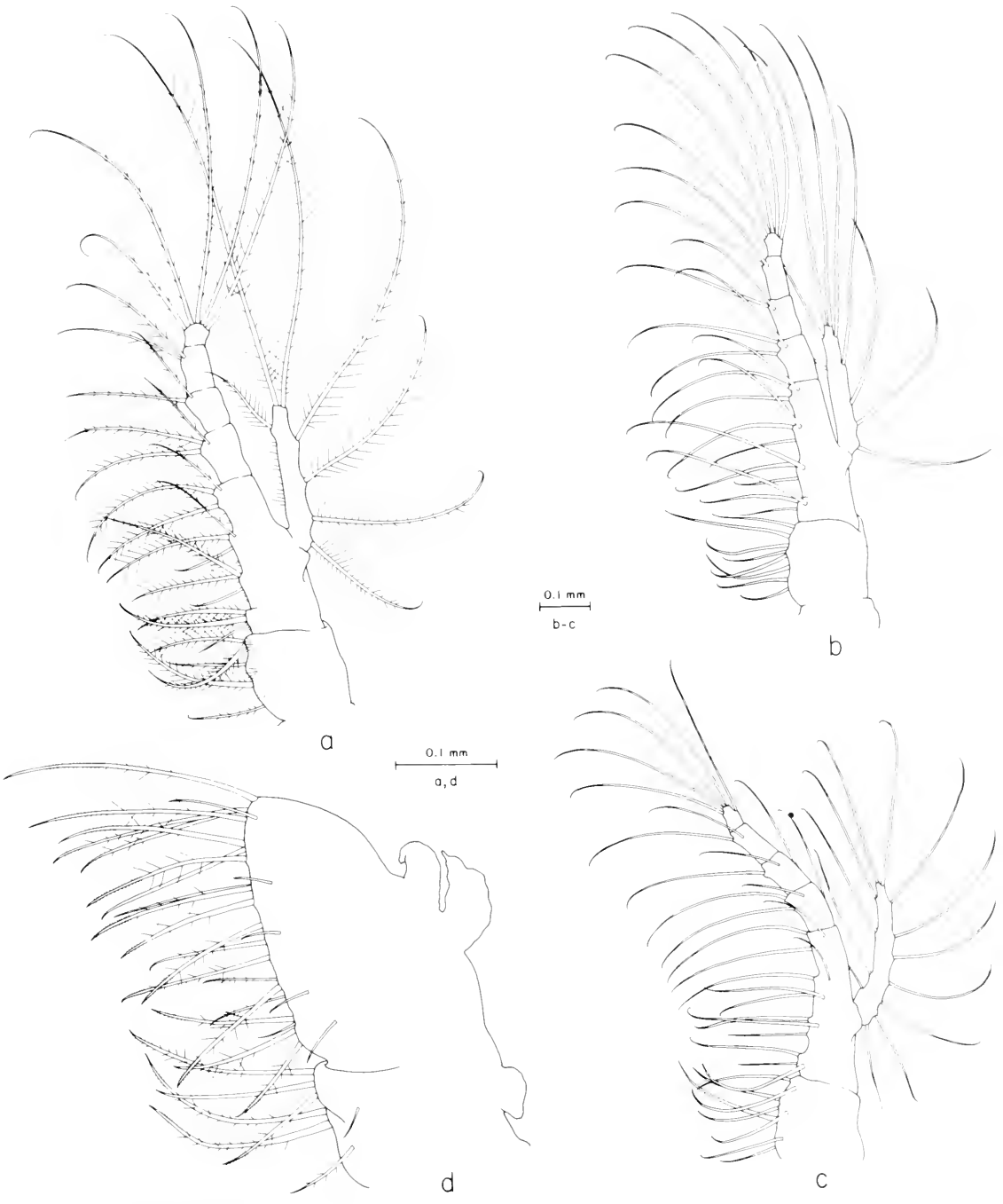

FIGURE 8.—*Sergestes similis*. First maxilliped: a-b, protozoea I, III; c, zoea I; d, postlarva I; setules omitted on b and c.

pair small ventolateral spines proximal to uropods; smooth ventral spines of telson relatively larger than in stage I.

Antennule (Fig. 2g) with proximal of 3 segments without subdivisions and segment 2 with 5 setae, otherwise setation unchanged.

Mandibles (Fig. 4f) usually with 3 and 6 spines on right and left cutting edges, 1 of 10 larvae

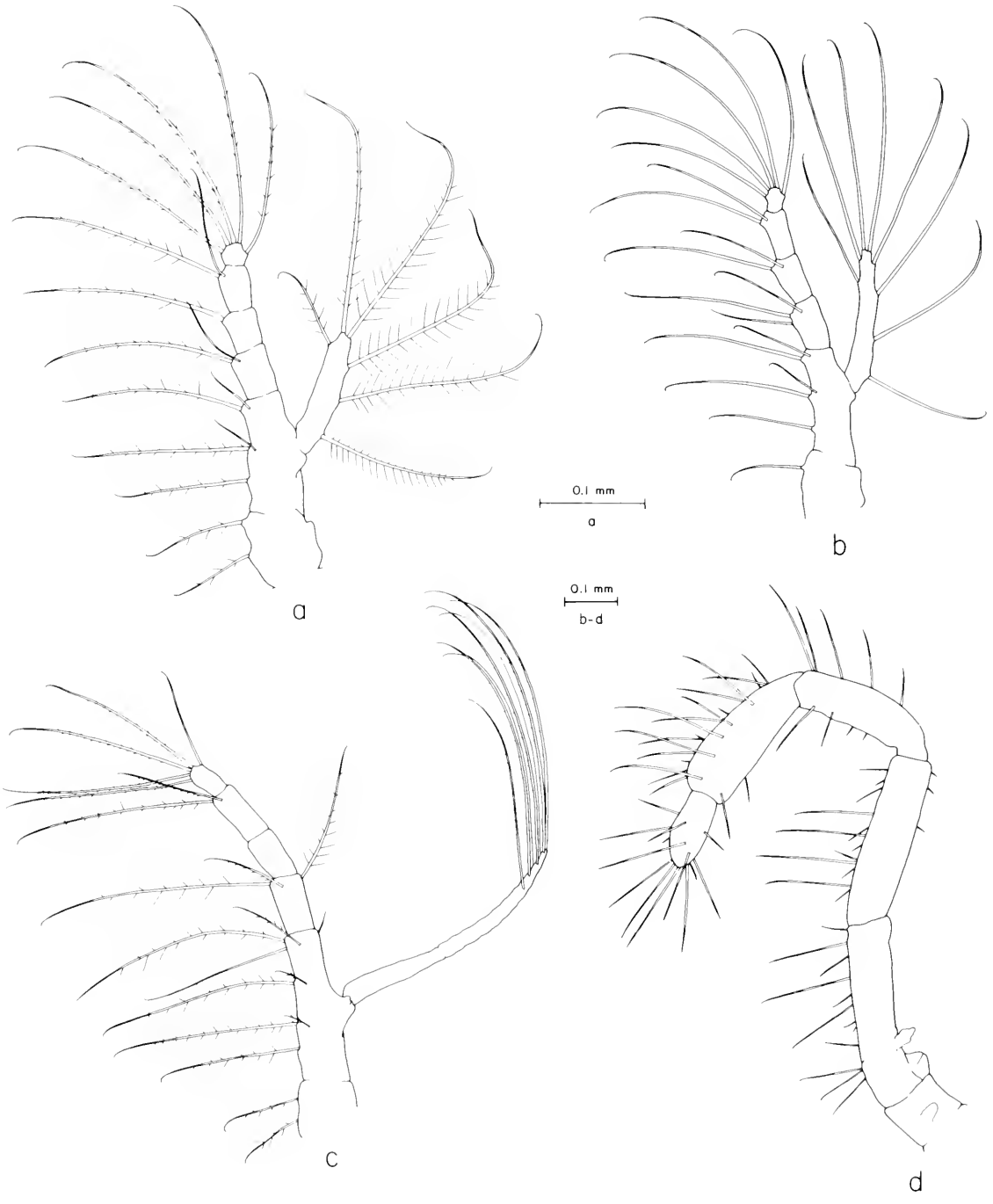

FIGURE 9.—*Sergestes similis*. Second maxilliped: a-b, protozoea I, III; c, zoea I; d, postlarva I; setules omitted on b.

FIGURE 10.— *Sergestes similis*. Protozoea II: a, dorsal view; b, lateral view.

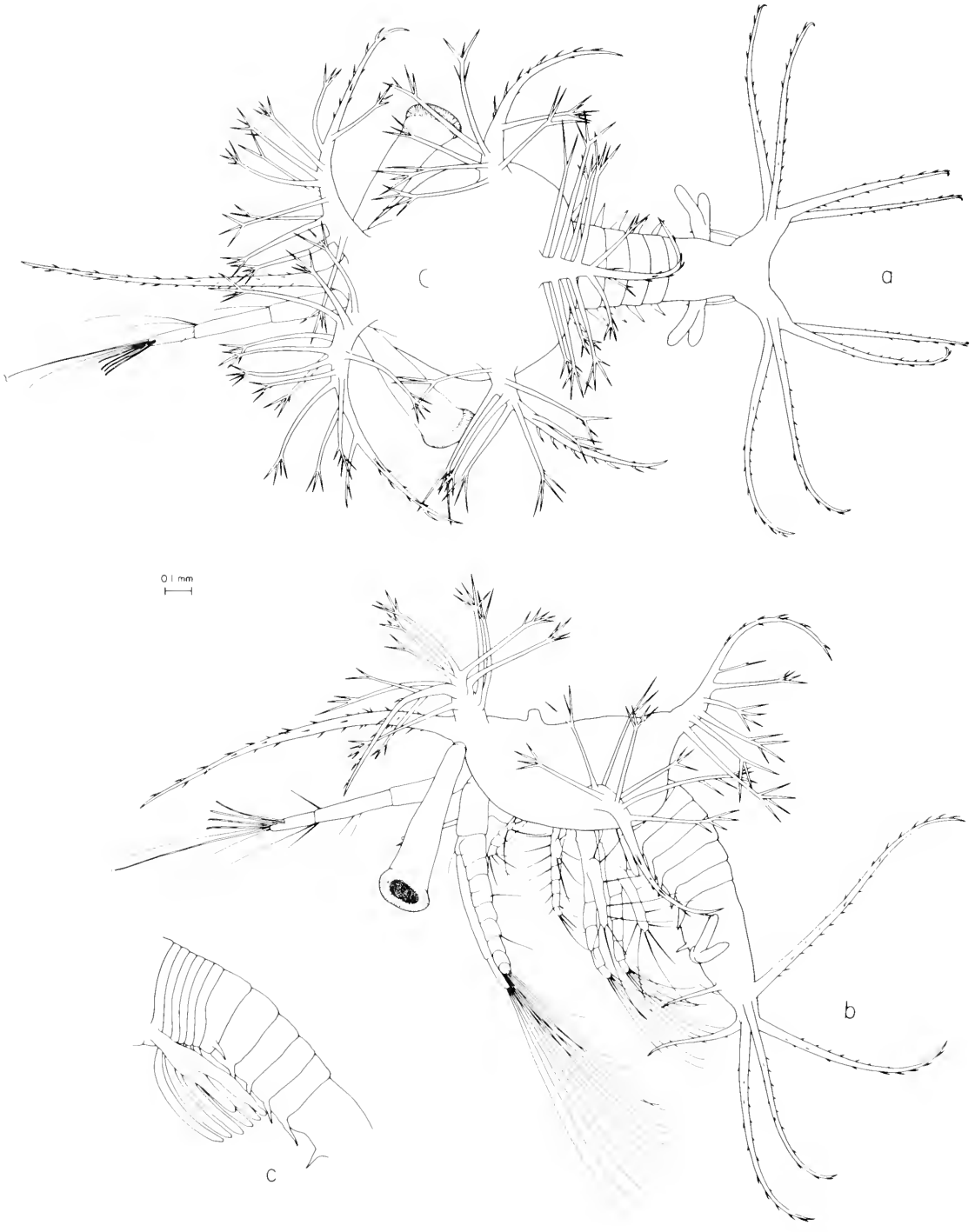

FIGURE 11.—*Sergestes similis*. Protozoea III: a, dorsal view; b, lateral view; c, third maxilliped and thoracic legs of late stage larva.

with armature of stage II, long spine nearest incisor teeth on right mandible separated from other long spines by several small teeth.

Maxillule (Fig. 6c) with 7 setae on both basal and coxal endites; as in earlier stages distal stout seta on basal endite with long basal spinules, other stout setae with short spinules.

Maxilla with setation of 9-5-6-5 on medial lobes, rarely with 8 setae on proximal lobe of coxal endite.

First maxilliped (Fig. 8b) with 9 setae on exopod.

Second maxilliped (Fig. 9b) with endopod setation of 3-2-2-5 and exopod with 8 setae; coxa with 1 or 2 setae.

Third maxilliped and thoracic legs 1-5 (Figs. 11c, 12a, d) biramous, unsegmented, and nonsetose with exopod slightly longer than endopod.

Zoea I (Figs. 13, 14a)

Body length: 3.25 mm (0.13).

Carapace altered with change in phase, now with 10 spines including rostrum, 1 pair supraorbital, 1 pair hepatic, 2 pairs lateral, and 1 posterodorsal, all spines armed only with spinules except rostrum which bears a strong basal dorsal spine with spinules; dorsal organ present in zoeal phase but smaller than in preceding stages. Eyes with long slender stalk bearing single ventral papilla in both stages of phase.

Abdomen of 6 segments with following armature: segments 1-5 with 1 pair lateral spines which decrease in length posteriorly, segments 1-6 with 1 posterodorsal spine longest on segments 3-5, segment 6 with 1 pair small ventrolateral spines and segment 1 with 1 pair triangular dorsolateral processes; posterodorsal and lateral spines armed with spinules, lateral spines of segments 1 and 2 with relatively long spinules proximally on posterior margin, segments with dorsal and lateral setae as figured. Telson (Fig. 15e) slender with 1 pair lateral spines on rounded margin and produced distally into 2 long slender spines which bear 4 spinules near one-third their length and tiny spinules distally.

Antennule (Fig. 2h) with peduncle unsegmented and with following armature: basal lateral spine; 13-16, usually 15, long plumose setae along inner, outer, and distal ventral margins; smaller setae distributed near basal spine and along dorsal surface of peduncle in clusters of 2-2-3-1-3. Flagella unsegmented; outer flagellum with 3 small spines and 1 seta distally, and dorsal tier of 6 aesthetascs near two-thirds the length of flagellum; inner ramus very small with 2 terminal spines.

Antenna (Fig. 3f) with scale (exopod) slender bearing 1 small subterminal ventral seta, 1 subterminal seta on outer margin, and 10 or 11, usually 11, setae on distal and inner margins, all setae with setules, terminal setae relatively stout and graded in size from short lateral to long medial seta; flagellum (endopod) with about 8 segments, proximal segment about the length of scale, distal segment with 4 terminal spines, 1 seta projecting laterally from each side, and 1 seta directed anteriorly; a strong spine with basal spinule appears on inner margin of flagellum before midpoint of segment 1 and distally on segment 6.

Mandibles (Fig. 4g) with 4 and 7 relatively long spines on right and left blades between incisor teeth and molar surfaces, bud of palp present. Labrum (Fig. 4k) with anteroventral spine present but shorter than in preceding phase.

Maxillule (Fig. 6d) with 11 setae on basal endite.

Maxilla (Fig. 7c) with exopod modified bearing 1 long plumose seta on proximal lobe and 4 small processes approximately in position of plumose setae of preceding stage; endopod unchanged; medial lobes with setation of 9-5-6-6.

First maxilliped (Fig. 8c) with form as in protozoeal phase; exopod with 13 marginal setae; endopod with setation of 4-3-2-5; basis with 13 and coxa with 8 setae.

Second maxilliped (Fig. 9c) somewhat modified, long flexible exopod with 7 or 8, rarely 8, setae and resembling exopod of thoracic leg rather than form of preceding phase; endopod 4-segmented with 3-0-2-5 setae; basis with 9 and coxa with 2-4 setae.

Third maxilliped (Fig. 12b) functional and pediform; exopod with 19-23, usually 21, setae; endopod 4-segmented, usually with setation of 3-4-4-5, rarely with 5 setae on segment 2; basis with 4 setae, coxa nonsetose.

Legs 1-5 functional; legs 1-3 (Fig. 12e) similar, shorter than third maxilliped; exopods with 20-22, frequently 21, setae; endopods 4-segmented with 3-4-4-4 setae and bases with 3 or 4 setae. Legs 4 and 5 (Fig. 16c, d) smaller than first three pairs; exopods with 17-19 setae; endopods

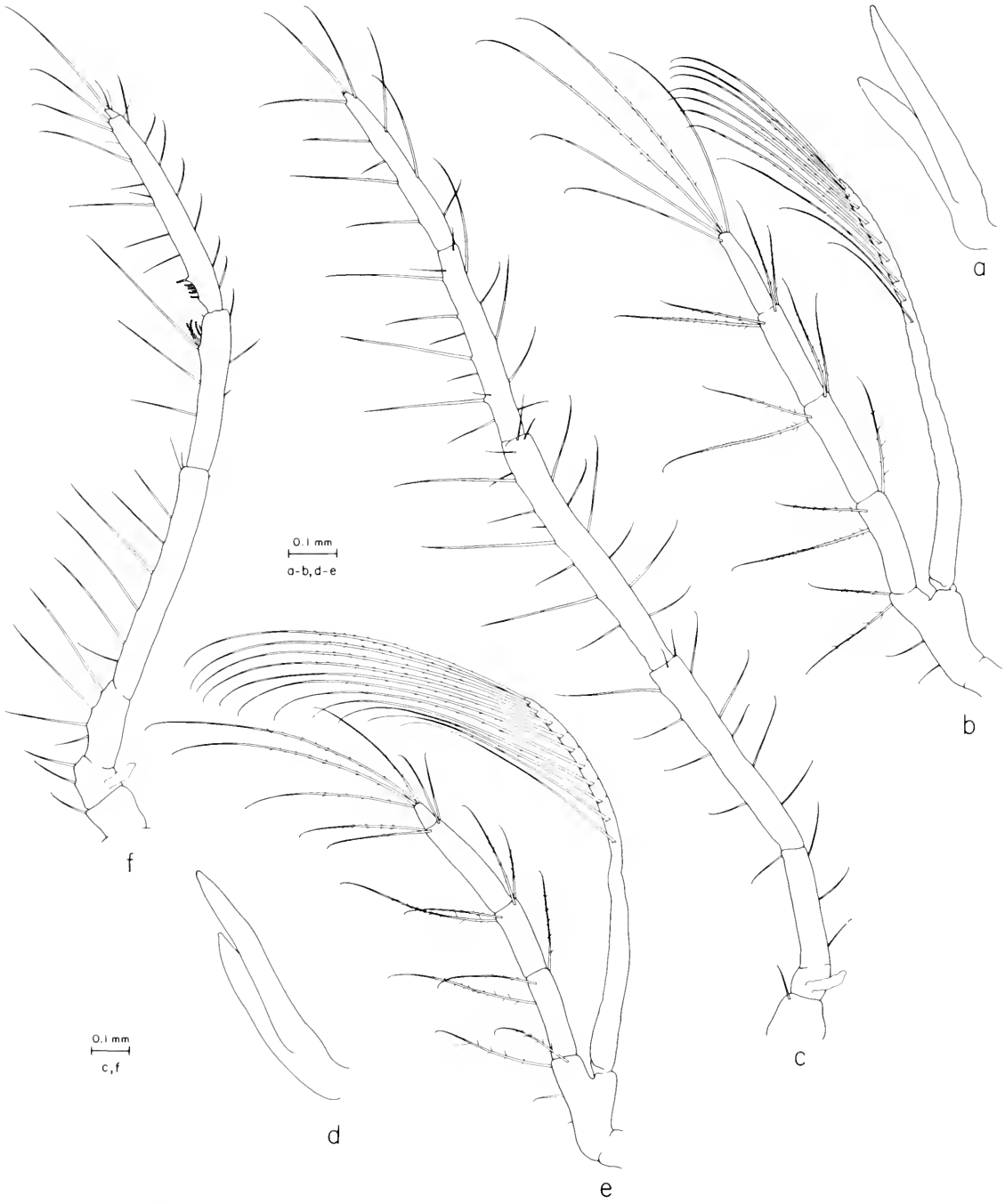

FIGURE 12.—*Sergestes similis*. Third maxilliped: a, protozoea III; b, zoea I; c, postlarva I. Leg 1: d, protozoea III; e, zoea I; f, postlarva I.

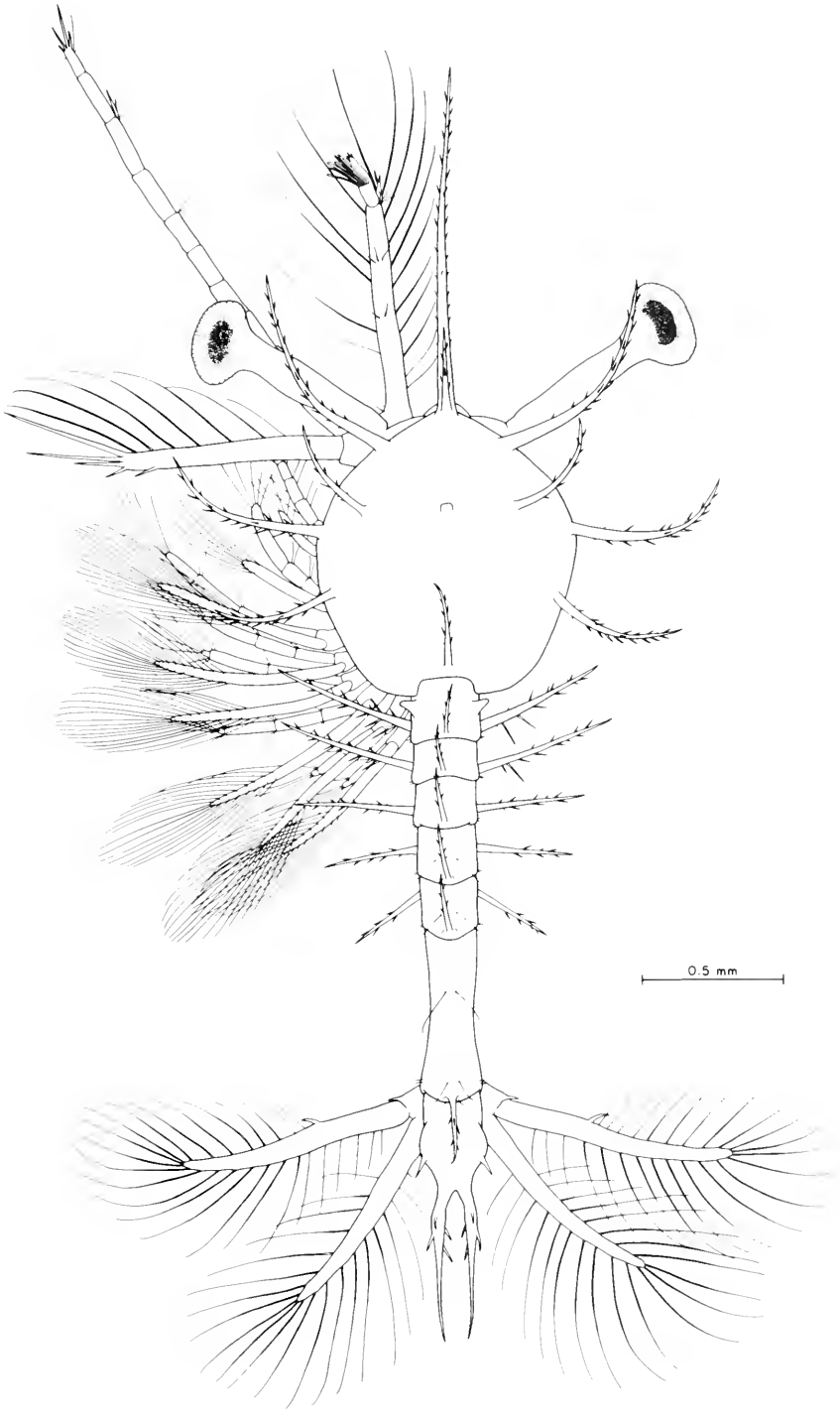

FIGURE 13.—*Sergestes similis*. Zoea I, dorsal view.

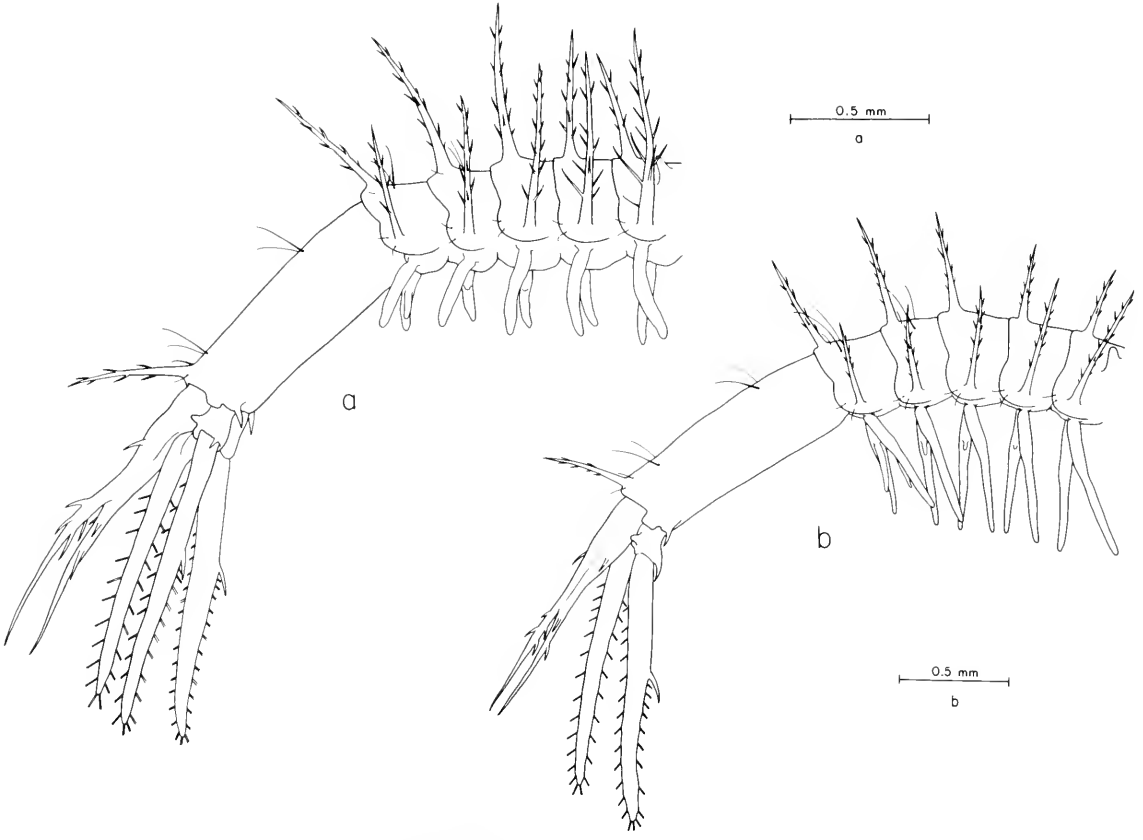

FIGURE 14.—*Sergestes similis*. Abdomen, lateral view: a, zoea I; b, zoea II.

3-segmented with 3-3-4 setae on leg 4, rarely 4 setae on segment 2, and 2-3-4 setae on leg 5; bases with 1 seta, coxae nonsetose.

Pleopods (Fig. 15a) present on abdominal segments 1-5 and variable in size within stage; exopods nonsetose decreasing in length from pleopod 1 to 5; pleopod 5 with nonsetose endopod about two-thirds length of exopod, pleopod 4 with small bud of endopod, pleopods 2 and 3 sometimes with some swelling in position of endopod.

Uropods with rami articulated; protopod with lateral spine and posterior projection (Fig. 14a); exopod and endopod long, slender, and fringed with plumose setae except proximal to smooth spine on lateral margin of exopod.

Zoea II (Figs. 14b, 17)

Body length: 4.42 mm (0.20).

Carapace, abdomen, and telson (Fig. 15f) with armature as in preceding stage; spines shorter relative to size of larva and lateral spines of abdominal segments 1 and 2 without long posterior spinules.

Antennule (Fig. 2i) with peduncle bearing 16-19, usually 17 or 18, marginal plumose setae and small setae in clusters of 3-4-3-1-3; outer flagellum with 1 distal seta and usually unsegmented, sometimes constricted at two points distal to tier of 6 aesthetascs, rarely with weak sutures; inner ramus without spines.

Antenna (Fig. 3g) with scale armed with long subterminal spine on outer margin bearing spinules, a small subterminal ventral seta, and 14 or 15 marginal plumose setae, terminal setae no longer stout; flagellum long, with 19-25 segments in three reared larvae, terminal segment with 2 spines and 3 setae, 1 seta projects laterally from each side.

Mandibles (Fig. 4h) with armature unchanged; palp larger than in zoea I, unsegmented and nonsetose. Labrum with short remnant of anteroventral spine.

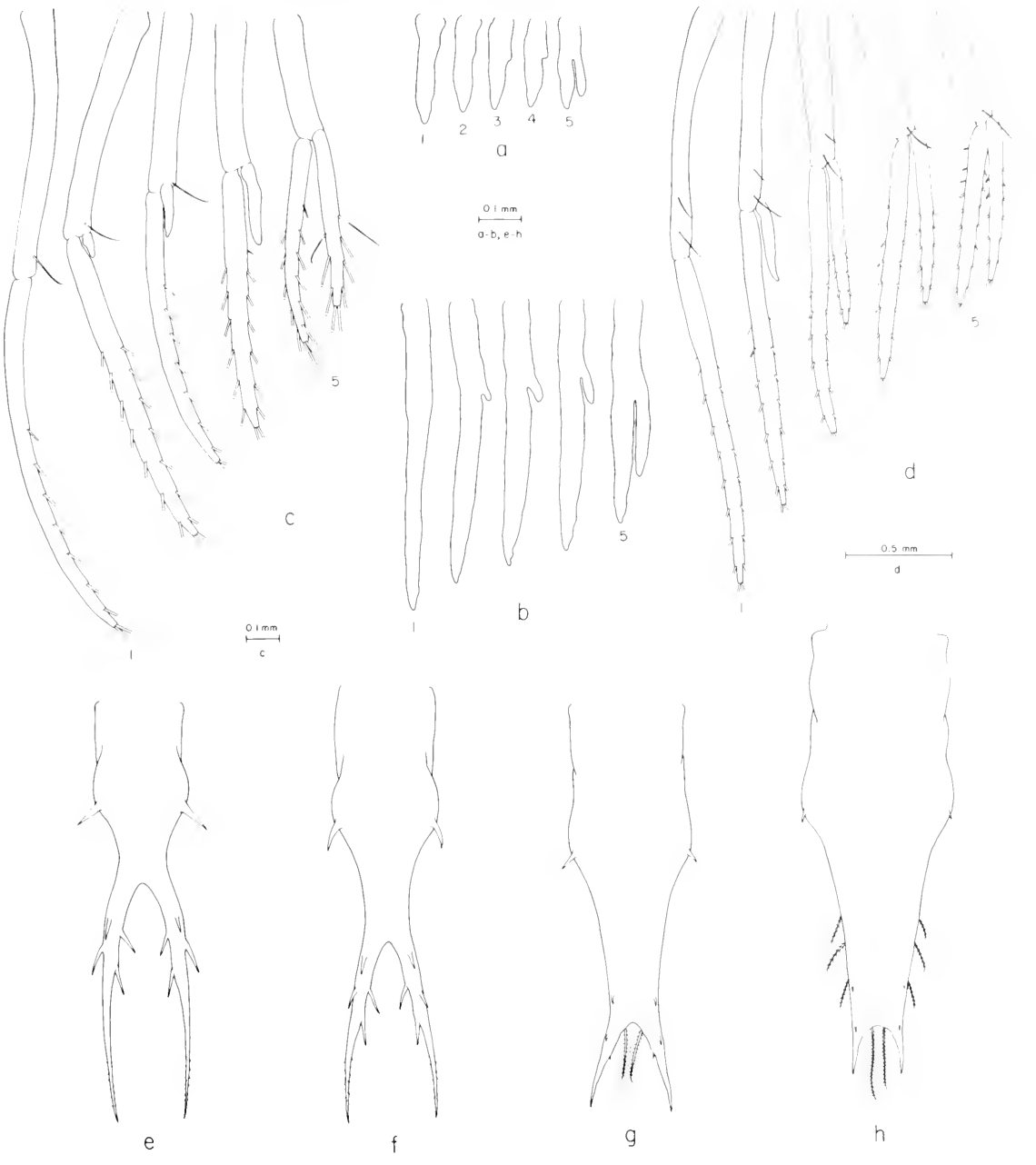

FIGURE 15.—*Sergestes similis.* Pleopods: a-b, zoea I-II; c-d, postlarva I-II. Telson: e-f, zoea I-II; g-h, postlarva I-II.

Maxillule with 12 or 13, usually 12, setae on basal endite and 8 or 9 setae on coxal endite.

Maxilla unchanged except that exopod relatively larger with small processes now tiny.

First maxilliped with 13 or 14, usually 13, setae on exopod.

Second maxilliped with endopod setation of 4-2-3-5, rarely 5 and 4 setae on segments 1 and 3; exopod with 7 setae; basis with 9 or 10 and coxa with 3 or 4 setae.

Third maxilliped with 4 or 5, rarely 4, setae on distal segment of endopod and 3 setae on basis.

Legs 1-3 with endopod slightly longer than exopod, legs 2 and 3 with distal margin of

endopod segment 3 swelling in formation of chela (Fig. 16a); exopods with 20-24, usually 22, setae; endopods usually with setation of 3-4-5-4, rarely 5 and 4 setae on segments 2 and 3; bases with 3 or 4 setae. Leg 4 exopod with 18-21 setae, endopod usually with setation of 3-3-4, rarely with 2 and 4 setae on segments 1 and 2. Leg 5 exopod with 16-19 setae, endopod usually with setation of 2-3-4, rarely with 3 setae on segment 1.

Pleopods (Fig. 15b) nonsetose but longer than in preceding stage, exopods again decreasing in length from anterior to posterior pairs; pleopods 2-5 with endopod which increases in size posteriorly with variation in size within stage with age.

FIGURE 16.—*Sergestes similis*. Leg 2: a, zoea II; b, postlarva I. Leg 4: c, zoea I. Leg 5: d, zoea I. Legs 4 and 5: e-f, postlarva I-II.

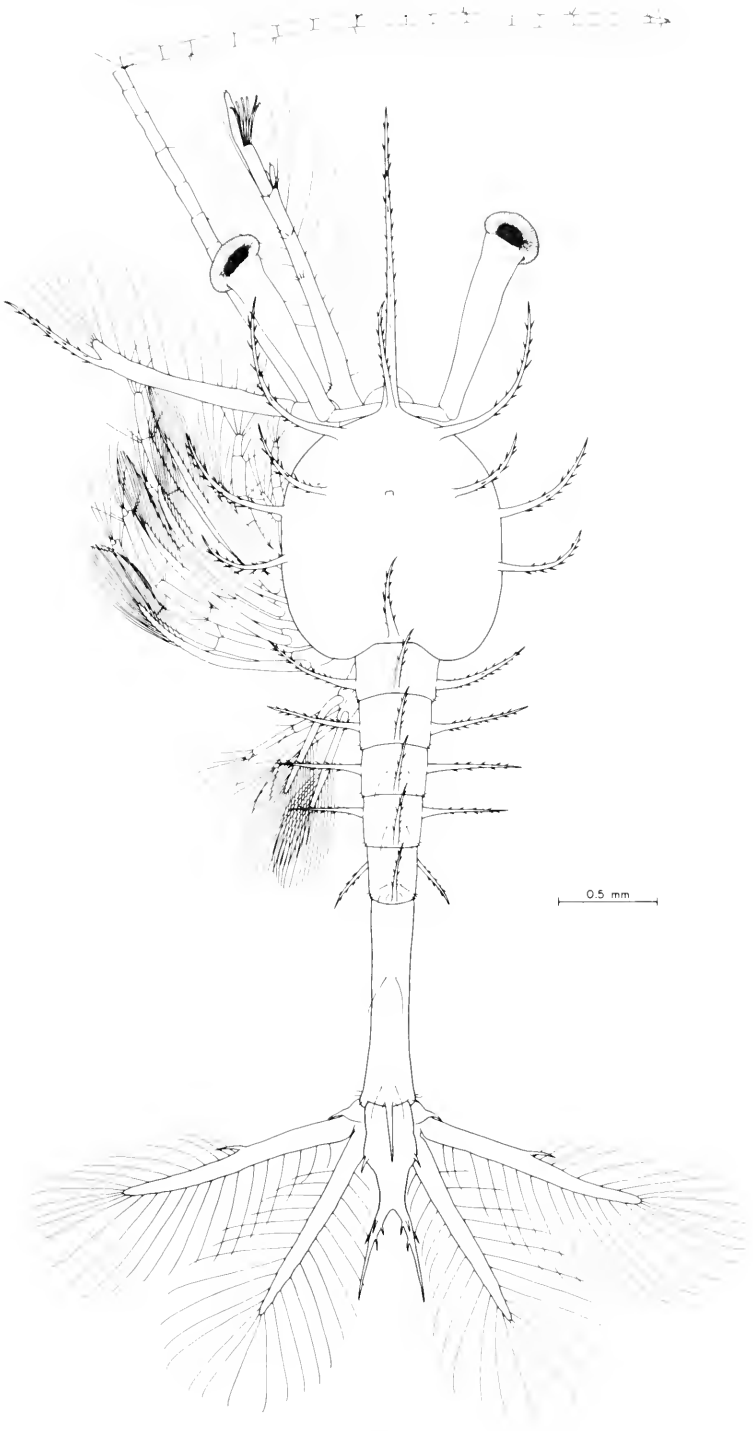

FIGURE 17.—*Sergestes similis.* Zoea II, dorsal view.

Postlarva I (Fig. 18a)

Body length: 5.07 mm (0.26).

Carapace with armature reduced, 2 pairs of lateral spines of preceding phase missing or only tiny remnants; rostrum, supraorbital, and hepatic spines, and posterodorsal spine shorter relative to length of carapace. Abdomen with lateral spines of segments 1-5 and posterodorsal spines of segments 1 and 2 small and without spinules. Telson (Fig. 15g) with posterior fork spines much shorter in relation to body of telson than in zoeal phase, with spinules reduced and with pair of plumose setae on inner margin near base of fork; relative length of terminal setae and fork spines vary within stage.

Antennule (Fig. 2j) with peduncle 3-segmented and fringed with marginal plumose setae, basal segment with statocyst and lateral spine; rows of small setae now situated on distal margins of segments; outer flagellum with 10 segments, proximal segments 1-3 with 1-2-6 medioventral aesthetascs, 6 aesthetascs of segment 3 set proximally on small protuberance; inner flagellum with 2 segments.

Antenna (Fig. 3h) with subterminal lateral spine of scale smaller than in zoea II, scale with 20-22 marginal setae; flagellum very long, about 2.6 times body length in one reared larva.

Mandibles (Fig. 4i) with cutting edges smooth between simplified incisor and molar processes, left mandible with notch opposing incisor tooth of right mandible; palp with 5-7 setae and sometimes indistinctly 2-segmented. Labrum without spine.

Maxillule (Fig. 6e) with endopod reduced to small nonsetose rudiment and with tiny vestige of exopod, basal and coxal endites with increased numbers of setae.

Maxilla (Fig. 7d) with endopod reduced to small nonsetose rudiment; scaphognathite (exopod) large with 17 or 18 marginal setae, 1 posterior seta relatively long; coxal and basal endites bifid, medial lobes with 2-2-4-4 to 6 setae.

First maxilliped (Fig. 8d) with small nonsetose exopod and endopod, coxa with medial setae and small epipodite, basis with broad flat medial lobe armed with setae along inner margin.

Second and third maxillipeds and legs 1-3 with small nonsetose remnant of exopod.

Second maxilliped (Fig. 9d) with endopod long, 5-segmented, recurved at articulation of merus and carpus, and armed with strong setae, articulation of ischium and basis indistinct if visible; coxa with bud of epipodite.

Third maxilliped (Fig. 12c) with endopod long, 5-segmented, and with strong marginal setae.

Leg 1 (Fig. 12f) with clusters of strong barbed setae at articulation of propodus and carpus, legs 2 (Fig. 16b) and 3 with small setose chela, leg 2 with small spine on lateral margin of ischium. Leg 3 slightly longer than first maxilliped. Legs 4 and 5 (Fig. 16e) reduced to irregular, nonsetose bifid rudiments.

Pleopods (Fig. 15c) with setose exopods; endopod of pleopod 5 setose, rarely endopod 4 with 1 or 2 terminal setae, as before endopods increase and exopods decrease in length from anterior to posterior pairs; protopod with 1 distal seta on inner margin of pleopods 1-3; endopods vary in size within stage.

Postlarva II (Fig. 18b)

Body length: 5.80 mm (0.20).

Carapace and abdomen with armature reduced in size, small posterodorsal spine of carapace may be missing and dorsal spines of abdomen segments 1 and 2 very small. Telson (Fig. 15h) with posterolateral spines reduced in length and usually with 3 pairs plumose lateral setae in addition to terminal pair.

Antennule with outer flagellum, in exuvia of one reared larva, with about 17 segments and increased number of aesthetascs on proximal segments; inner flagellum with 2 or 3 segments.

Antenna with subterminal lateral spine of scale smooth or with few spinules and reduced in length, scale with 24-28 marginal setae.

Mandibles with palp 2-segmented bearing 11-14, usually 11 or 12, setae.

Maxillule with endopod more distinctly shaped; vestige of exopod not present.

Maxilla with 25-27 setae on scaphognathite; endopod larger than in preceding stage with outer basal seta and sometimes inner seta; medial lobes with setation of 2-3-5 to 8-8 or 9.

First maxilliped with endopod, exopod, and epipodite larger than in postlarva I, rarely endopod slightly longer than exopod with some indication of segmentation.

Second and third maxillipeds and legs 1-3 without vestige of exopod; legs 1 and 2 with small ischial spine; legs 4 and 5 (Fig. 16f) more distinctly formed, nonsetose, and with leg 4 longer than leg 5.

Pleopods 3-5 (Fig. 15d) with setose endopods,

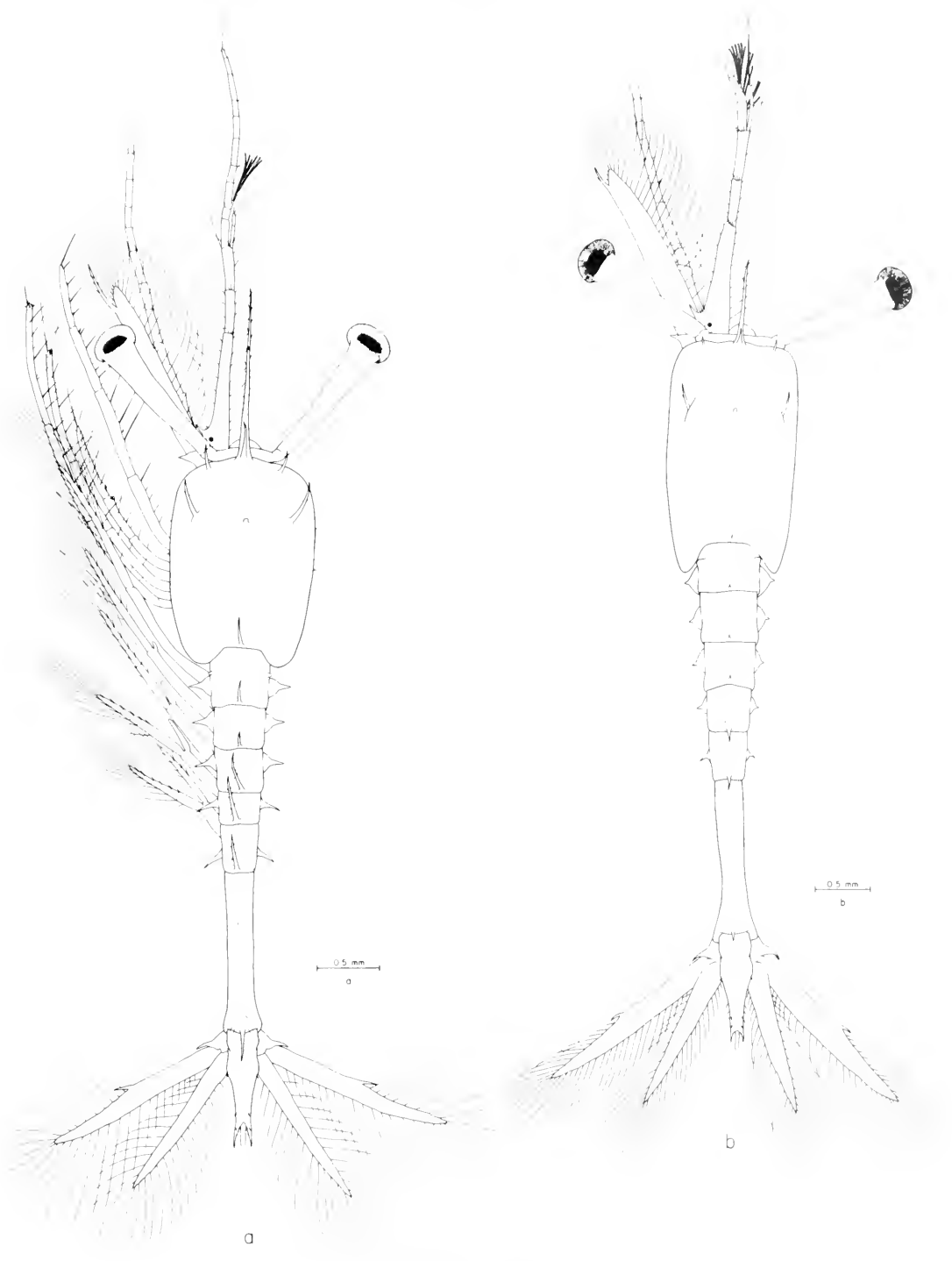

FIGURE 18.—*Sergestes similis*. a, postlarva I; b, postlarva II.

rarely endopod of pleopod 2 with 1 or 2 small setae; protopods of pleopods 1-3 with 2 setae; those of pleopods 4 and 5 with or without 1 seta on protopod.

DISCUSSION

Yaldwyn (1957) defined two subgenera, *Sergestes* s.s. and *Sergia*, within what he termed the rather unwieldy genus *Segestes* s.l. Recently, the subgenera were raised to full genera by Omori (1974). The species of *Sergestes* have specialized luminescent modifications of the gastrohepatic gland called organs of Pesta and are without cuticular pigmentation and dermal photophores, while species of *Sergia* are without organs of Pesta and, with some exceptions, have uniform cuticular pigmentation and often dermal photophores. The two genera are themselves divided into species groups, six in *Sergestes* and three in *Sergia*, which appear to be easily distinguished and are considered to be natural phyletic units (Judkins 1978).

The *arcticus* group includes only two species, *Sergestes arcticus* and *S. similis*, and is characterized by the morphology of third maxilliped, fifth pereiopod, antennular peduncle, and petasma (Yaldwyn 1957). *Sergestes similis* differs from *S. arcticus* in having a more slender and fragile body and antennular peduncle, in a longer and more upwardly directed rostrum, in proportions of posterior arthrobranchs above the third and fourth pereiopods, and in some proportions and armature of petasma and thelycum (Milne 1968).

The close relationship of *S. similis* and *S. arcticus* which has been inferred from adult morphology may also be seen in their larval morphology, especially in the shape of eye, in the ornate armature of protozoeal carapace, and in the armature of carapace, abdomen, and telson in the zoeal phase. Gurney and Lebour (1940) described larvae now known to be representative of all of the species groups within *Sergestes* s.l. and noted that the protozoea II and III of *S. arcticus* were very distinct in form of eye and peculiarly branched spines. They described some features of protozoea II and III, zoea I and II, and postlarva I of *S. arcticus* and gave figures of the second protozoea and zoea, with telson of postlarva I. They stated that the "brushlike endings" of the long spines on rostral, lateral, and posterior processes of protozoea II and on supraorbital, lateral, and posterior processes of protozoea III were most characteristic of the species. The protozoea II and III of *S. similis*, identified in this study, have the same distinctive armature of carapace spines.

The larval stages of *S. arcticus* discussed by Gurney and Lebour (1940) resemble the comparable stages of *S. similis* in the details they described and figured. Gurney and Lebour, however, do not deal with the structure of mouthparts and thoracic appendages; rather, they note that these appendages seem to be uniform throughout the genus and refer the reader to the earlier descriptions of *S. arcticus* by Wasserloos (1908) and Hansen (1922). Gurney, in a later work (1942), does figure the appendages of protozoea III of *S. cornutus*, an *atlanticus* group species, and they appear very similar to those of the same stage of *S. similis*.

The protozoeal stages of *S. arcticus* described by Wasserloos (1908), on the other hand, differ from those of *S. similis* in setation and/or segmentation of antennule, antenna, and mouthparts, but appendages are not figured; the armature of carapace differs in protozoea II and III on lateral and supraorbital processes, respectively. The species appear similar in described and figured features of the zoeal phase.

Hansen (1922) offered a brief summary of Wasserloos' description of the protozoeal phase and added both generic and specific comments, with figures, on the zoea and postlarva of *S. arcticus* from his own observations. He noted that the mouthparts of the protozoea are like those of the zoeal stages which he described in some detail but which do not always agree with details of the protozoeal phase described by Wasserloos. Hansen also noted that the rostrum in protozoea III is little modified from stage II, yet conspicuous secondary spines are lost in this molt. In the zoeal phase, *S. similis* larvae differ from those of *S. arcticus*, as described by Hansen, in segmentation of maxillule and first maxilliped.

Unfortunately, because the descriptions of *S. arcticus* by Wasserloos (1908) and Hansen (1922) were found to be inconsistent with each other and with that of Gurney and Lebour (1940), and they could not be interpreted with confidence, a detailed comparison with *S. similis* was not possible. A reexamination of the larval stages of *S. arcticus* is needed to detect specific differences that may exist between the apparently very similar *arcticus* group species.

Gurney and Lebour (1940) believed the elaborate protozoeal phase of *Sergestes* s.l. to be of particular importance, as it might "point to a satisfactory subgeneric grouping of the adults." They separated the second and third protozoeae of thirteen species of *Sergestes* s.l., representative of all of the nine species groups later defined by Yaldwyn (1957), into three types: *dohrni*, *ortmanni*, and *hispida*. The carapace has the same number of processes in all three types but the armature of the processes differs as follows: *dohrni* type with numerous long lateral spines on supraorbital, lateral, and posterior processes; *ortmanni* type with long spines on supraorbital processes but with long spines only at the bases of lateral and posterior processes on carapace; *hispida* type without long spines on supraorbital, lateral, or posterior processes, although there may be basal spines on lateral and posterior processes. Gurney and Lebour observed that the *ortmanni* armature seems to be derived from the *dohrni* type in that it retains long lateral spines on supraorbital processes.

These larval types do correspond with three divisions of species within *Sergestes* s.l. Of the species described by Gurney and Lebour (1940), the *hispida* type larvae all belong to the genus *Sergia*, while the *dohrni* and *ortmanni* types belong to *Sergestes*; *S. corniculum* is of the *ortmanni* type, but all other species of *Sergestes* identified are of the *dohrni* type. The zoeal stages could not be separated into groups which corresponded to the protozoeal types.

Gurney and Lebour (1940) noted that the *dohrni* type carapace was found in a number of species which were not supposed to be particularly closely related and which could not be grouped further by structure of the protozoeal phase. The identification of *S. similis* larvae has proved this untrue with respect to the *arcticus* group species, but apparently it does apply to species of the *atlanticus* group, the only other species group within *Sergestes*, or *Sergia*, all of whose protozoeal stages are identified. Gurney and Lebour described the larvae of *Sergestes atlanticus* and *S. cornutus*, the two species which comprise the *atlanticus* group, and observed that larval morphology did not corroborate the close relationship implied by the morphology of adult petasma. The carapace armature in protozoea II and III of the *arcticus* and *atlanticus* groups is compared in Table 1 to show the range of variation within each group; the species groups themselves are not considered to be closely related within the genus (Judkins 1972). *Sergestes arcticus* and *S. similis* may have the same armature in both protozoeal stages, while *S. atlanticus* and *S. cornutus* differ in each stage; all of the lateral spines of the *atlanticus* group have smooth tips rather than the brushlike endings characteristic of the *arcticus* group.

The difference in larval morphology within the *atlanticus* group is in accordance with the significant difference described by Foxton (1972) between *S. atlanticus* and *S. cornutus* in morphology of the organs of Pesta. This discrepancy was one of two exceptions noted by Foxton to a generalization that species of *Sergestes* that are the most similar in other adult diagnostic characters usually have identical or closely similar organs of Pesta; he does not note any difference between the *arcticus* group

TABLE 1.—Comparison of the number of long lateral spines which arm carapace processes in protozoea II and III of two species groups of *Sergestes*; the lateral spines have smooth tips in the *atlanticus* group and branching tips ("brushlike endings") in the *arcticus* group (descriptions of the *atlanticus* group and *S. arcticus* are taken from Gurney and Lebour (1940).

Carapace processes	*arcticus* group		*atlanticus* group	
	S. similis	*S. arcticus*	*S. atlanticus*	*S. cornutus*
Protozoea II:				
Rostrum	6 in 3 pairs	as *similis*	7 rather irregularly arranged	8 in 4 pairs + 2 ventral
Lateral, each	6-8, usually 7	[1]7	9	8
Posterior	4-8, with 3 large pairs	6 in 3 pairs	6, process swollen basally	4 in 2 pairs
Protozoea III:				
Rostrum	with spinules only	as *similis*	3 ventral	7 ventral
Supraorbital, each	9-14, usually 10-12; processes curve posterolaterally	9, orientation as in *similis*	ca. 15; processes curve inward to meet and overlap	12-19, processes directed anterolaterally
Lateral, each	5-8, usually 7	7	17-20	12-14
Posterior	7-13, usually 10-12 in 5-6 pairs	10 in 5 pairs	16 arranged in circle on large basal swelling	8 in 4 pairs

[1]Gurney and Lebour (1940) report eight long spines on the lateral carapace process, but their figure shows seven with brushlike endings and the simple spinulose tip of process, the common armature in *S. similis*.

species in morphology of this feature. The correspondence between variation in morphology of protozoeal stages and organs of Pesta within the two species groups indicates that, with identification of additional species, larval morphology may prove useful in the study of interspecific relationships within *Sergestes*, as predicted by Gurney and Lebour (1940).

The larvae of *S. similis* were also compared with those of *hispida* type *Sergia lucens* (Omori 1969), one of the seven species comprising the *challengeri* group. They were found to differ in body armature, as expected from difference in protozeal type, in form of telson, and in development of some appendages, as shown in Table 2. They also differ in number of naupliar stages. Four distinct stages were observed in the naupliar phase of *Sergestes similis*, while in *Sergia lucens* nauplius I and II were found and the latter developed gradually to molt into protozoea I. When this finding is coupled with the observations by Nakazawa (1916, 1932), they suggest that there are zero to two molts during the naupliar phase of *S. lucens*. An assessment of the significance of these observations requires additional knowledge of larval development within the two closely related genera and their species groups.

ACKNOWLEDGMENTS

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TABLE 2.—Some differences between larvae of *Sergestes similis* and *Sergia lucens*.

Feature	*Sergestes similis*	*Sergia lucens*
Carapace armature:		
Protozoea I	anterolateral process branches to 3 spines posterodorsal process a single spine with basal spinules	anterolateral process branches to 4 spines posterodorsal process branches to 3 spines
Protozoea II	all processes with long spines which branch to spinules distally	all processes with small spinules only
Protozoea III	rostrum with small spinules, armature of other processes as in II	as in II
Zoea I-II	with 2 pairs lateral spines	with 3 pairs lateral spines
Postlarva I	lateral spines remnants only, other spines present	rostrum and small posterodorsal spine present; supraorbital spine and basal spine of rostrum sometimes present, lateral and hepatic spines missing
Abdomen armature:		
Zoea I-II	lateral spines decrease in length posteriorly, spines 1 and 2 with relatively long spinules in I	lateral spines increase in length posteriorly, without long spinules in I
Telson:		
Zoea I-II	fork with 2 outer and 2 inner spinules, invagination does not reach lateral spines	fork with 1 outer and 5/6 inner spinules in I, with 2 outer spinules in II, invagination about as deep as lateral spines
Postlarva I	fork relatively wide with tiny spinules	fork narrow, with 2 large inner setae
Antennule:		
Zoea I-II	outer flagellum unsegmented in rarely 2- or 3-segmented in II and shorter than peduncle	outer flagellum 2-segmented in I, ca. 8-segmented in II, and longer than peduncle
Antenna:		
Zoea I	endopod 8-segmented and longer than rostrum	endopod 2-segmented and shorter than rostrum
Mandible:	palp appears in zoea I	palp appears in zoea II, rarely in zoea I
First maxilliped:		
Zoea I-II	exopod with 13 or 14 setae	exopod with 12 setae

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GROWTH OF JUVENILE ENGLISH SOLE, *PAROPHRYS VETULUS*, IN ESTUARINE AND OPEN COASTAL NURSERY GROUNDS

ANDREW A. ROSENBERG[1]

ABSTRACT

The growth of English sole juveniles, during 1978-79, from estuarine and open coastal nursery grounds on the Oregon coast is described in detail. Counts of fortnightly growth rings on otoliths were used to determine size-at-age. Mean growth rates were similar for the two areas, but variability in size-at-age was much greater among fish captured in the estuary.

Back calculation of individual growth, using radial measurements on the otoliths, showed that growth proceeds linearly during the first year of life. Differences in average growth among individual fish account for the high variability in size-at-age among fish found in the estuary. Fish from the estuary grew slightly faster, on average, in 1979 compared with 1978.

The settlement date of English sole larvae to the benthic habitat, determined from age data, occurred over the winter and spring in the open coastal nursery area. In the estuary, settlement was concentrated in the early winter.

The life cycle of many marine fishes contains a stage in which the juveniles of the species are concentrated in a specific area or nursery ground where the adults are uncommon. On both the east and west coasts of North America, estuarine areas are extensively used as nursery grounds for a large number of species (Gunter 1961; Pearcy 1962; McHugh 1967; Haedrich in press). Many east coast fishes are considered to be dependent on estuarines during early life. On the west coast, estuarine dependence has not been clearly demonstrated (McHugh 1967; Pearcy and Myers 1974).

The high productivity of estuarine areas, providing improved growth conditions for juvenile fish, the apparent lack of large predators, and reduction of competition among age groups of a species are frequently invoked explanations for estuarine dependence (Haedrich in press; Kuipers 1977). Unfortunately, it is difficult to test these hypotheses for most species of fish, because it is uncommon to find a species which uses both estuarine and nonestuarine nursery environments in a small geographic area.

The commercially important pleuronectid *Parophrys vetulus* Girard, found off the Oregon coast, uses both estuarine and nonestuarine habitats as nursery areas during the first year of life (Laroche and Holton 1979). This study examines the growth of the English sole, *Parophrys vetulus*, juveniles from two nursery grounds: the Yaquina Bay estuary (Pearcy and Myers 1974) and the open coastal area off Moolach Beach, Oreg. (Laroche and Holton 1979).

Size-at-age data, obtained from daily and fortnightly growth ring counts on otoliths, are used to detail growth during the first year. Daily growth rings on otoliths have been documented in many species of fish (Pannella 1971; Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Coble 1977). Pannella (1974) reported fortnightly banding patterns in several species as well. Laroche et al. (1982) have provided laboratory evidence for the daily periodicity of growth rings on *P. vetulus* otoliths.

METHODS

Sampling was conducted from September 1978 through September 1979 at Moolach Beach and Yaquina Bay. The sampling stations are shown in Figure 1. A tow was made at each station with a 1.5 m wide beam trawl lined with 7 mm stretch mesh. Tows were for 5 min in Yaquina Bay and for 10 min at Moolach Beach. The beam trawl was equipped with a 1.0 m circumference odometer wheel to measure distance travelled on the bottom. Measurements of bottom temperature and salinity were made at each station.

All fish captured were preserved in a strongly buffered 10% solution of Formalin[2] in seawater.

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

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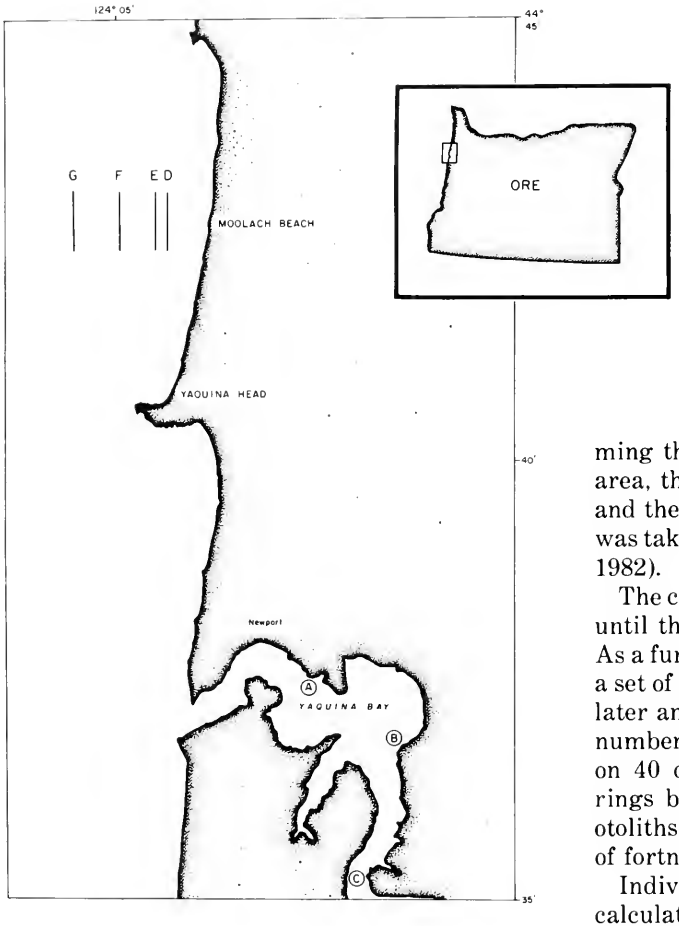

FIGURE 1.—The study area. Sampling stations are indicated by the letters A through G.

In the laboratory, all fish were identified and measured for standard length (SL). Both saccular otoliths were removed from each English sole. In cases where large numbers of *P. vetulus* were captured, individuals were selected to cover the size range of the sample. The otoliths were mounted on microscope slides in the synthetic mounting medium Protexx.

One otolith from each fish was ground on 600 grit carborundum paper to a thin section along a sagittal plane through the nucleus. The sections were examined under 250× magnification, using either bright-field or polarized illumination. Counts of fortnightly rings were made on each otolith. No fortnightly rings could be detected in the central area of the otoliths, which apparently represents the time the larvae are in the plankton. Therefore, daily rings were counted from the nucleus out to the first fortnightly ring. The actual age of each fish was calculated by summing the number of daily rings in the nuclear area, the number of fortnightly rings times 14, and the mean age of first ring formation, which was taken to be 5 d for this species (Laroche et al. 1982).

The count of rings on each otolith was repeated until the same count was obtained three times. As a further check on the accuracy of the counts, a set of 42 otoliths was recounted several months later and a mean error computed. Counts of the number of daily rings between fortnightly rings on 40 otoliths and the number of fortnightly rings between consecutive annual rings on 15 otoliths from older specimens were made as tests of fortnightly periodicity.

Individual growth curves of 25 fish were back calculated by making radial measurements to every other fortnightly ring along the same axis from the nucleus to the anterior edge of the otolith. From these measurements and the linear relationship between otolith radius and standard length of the fish,[3] lengths-at-age for the various points in the life of an individual were calculated.

RESULTS

Counts of daily rings between fortnightly rings yielded a mean of 13.95 with a standard deviation of 0.68. The mean number of fortnightly rings between consecutive annual rings was 26 with a standard deviation of 1.13. The mean difference between repeated counts of fortnightly rings made a substantial period of time apart was 1.45 rings. Figure 2 shows the daily and fort-

[3]A regression of standard length on anterior otolith radius was performed on 60 data points. The resulting equation was: $Y = 0.86x + 4.5$, where Y is standard length in mm and x is the distance from the nucleus to the anterior edge of the otolith in arbitrary units. r^2 for this regression is 0.98.

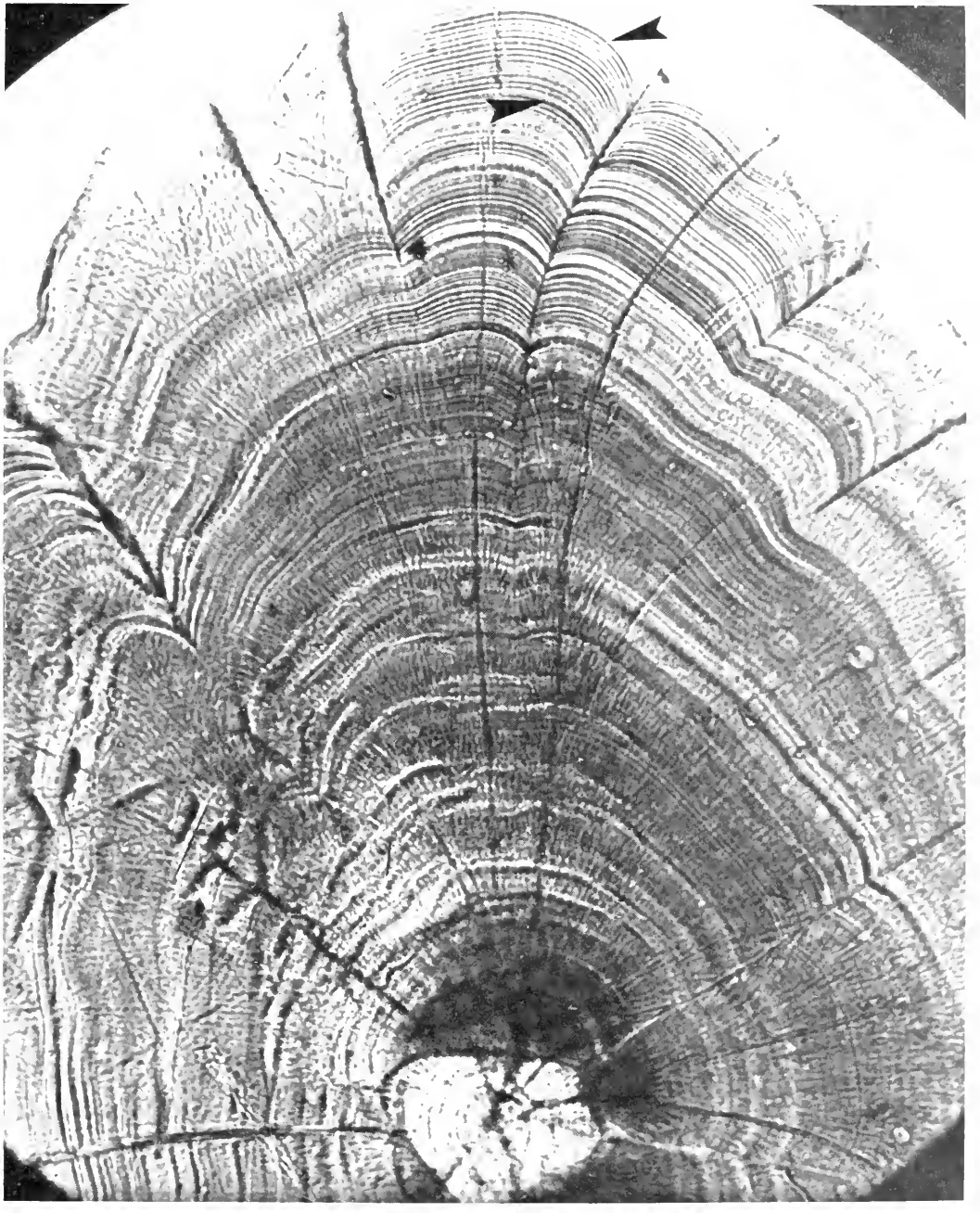

FIGURE 2.—An otolith from a 110 mm SL *Parophrys vetulus* captured in Yaquina Bay. Arrows indicate clear fortnightly rings. There are 21 fortnightly rings on this otolith. The actual age was calculated to be 363 d (see text).

nightly patterns of a *P. vetulus* otolith. The first fortnightly ring is formed consistently when the fish is 60 to 75 d old, i.e., the beginning of the metamorphic period (Rosenberg and Laroche 1982).

Basic growth data for the two nursery areas were obtained from size-at-age information. The data for 218 fish captured at Moolach Beach (Fig. 3) show that there are two linear portions of the data, with different slopes, separated by an

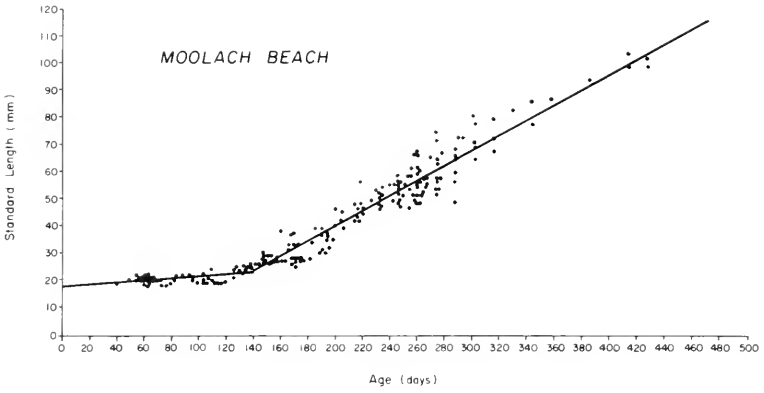

FIGURE 3.—Size-at-age data for *Parophrys vetulus* captured in the Moolach Beach nursery area.

inflection point. There is no evidence of an upper asymptote in the data, so the use of growth models such as the Gompertz or von Bertalanffy equations is inappropriate. A least squares multiple regression on these data was performed using the following model:

$$Y = B_0 + B_1X + B_2A_1 + B_3A_2 + E \quad (1)$$

where Y is the standard length in millimeters, X is the age in days, A_1 is a dummy variable whose value is zero to the left of the inflection point and one to the right of the inflection point, and A_2 is equal to X times A_1, i.e., the interaction term. The B terms are the regression coefficients and E indicates the error terms. The point of inflection which produced the smallest residual sum of squares was found to be 140 d for the Moolach Beach data. The fitted equation is:

$$Y = 16.87 + 0.051X - 32.92A_1 + 0.23A_2.$$

An analysis of variance for the regression (Table 1A) shows that a good fit was obtained with this model, and the data set has a relatively low estimated variance. The slopes of the regression below and above 140 d were computed as 0.051 and 0.279, respectively. These slopes are estimates of the mean growth rate per day for juvenile *P. vetulus* utilizing the Moolach Beach nursery area. The lower portion of the data, below 140 d of age, shows a plateau in growth attributed to the metamorphic period (Rosenberg and Laroche 1982).

Regression of the size-at-age data for Yaquina Bay juveniles (Fig. 4: 186 data points) yields the fitted equation:

$$Y = 13.01 + 0.083X - 33.45A_1 + 0.201A_2.$$

The analysis of variance for this model (Table 1B) once again shows that a good fit was obtained, but the estimated variance is much higher than for the Moolach Beach data. The inflection point with the smallest residual sum of squares was also 140 d of age for the Yaquina Bay data. The slopes below and above the inflection are 0.083 and 0.284, respectively.

The first step in comparing the regression lines of growth for English sole from the two nursery grounds was to test for statistical equality of variances. This was done by examination of the ratio of the mean square errors of the fitted regressions, 19.88 for the Moolach Beach data and 95.01 for the Yaquina Bay data. The ratio is distributed as F(184:216) and the variances are significantly different at the $P = 0.001$ level. Since the variances are unequal, statistical tests for equality of slopes or intercepts are not strictly valid (Scheffe 1959). However, the slopes are similar, 0.279 and 0.284.

Back-calculated growth for individuals from both areas are in good agreement with growth

TABLE 1.—Analysis of variance for the least squares multiple regression analysis of size-at-age data.

A. Moolach Beach regression:

$Y = 16.87 + 0.015X - 32.92\ A_1 + 0.23\ A_2$

Multiple $R = 0.975$
$R^2 = 0.950$

Source	DF	Sum of squares	Mean square
Regression	3	80815.2	26938.4
Residual	214	4253.7	19.9

F value = 1355.0

B. Yaquina Bay regression:

$Y = 13.01 + 0.083X - 33.45\ A_1 + 0.201\ A_2$

Multiple $R = 0.943$
$R^2 = 0.890$

Source	DF	Sum of squares	Mean square
Regression	3	139575 6	46525.2
Residual	182	17308.1	95.1

F value = 489.3

FIGURE 4.—Size-at-age data for *Parophrys vetulus* captured in the Yaquina Bay nursery area.

estimates from the size-at-age data (Figs. 5, 6). The plots are, in general, linear. Slight changes in slope do occur in all the lines. This may indicate small variations in individual growth through the juvenile period, changes in the linear nature of the relationship between otolith growth and overall fish growth, or measurement error. By inspection, these variations do not occur at coincident times among individuals. For the Moolach Beach data (Fig. 5), the average slope of the eight lines ranged from 0.20 to 0.28. Average growth was not significantly different in the 2 yr (nonparametric rank sum test).

Individual growth back calculated from the otoliths of 16 fish captured in Yaquina Bay range in average slope from 0.19 to 0.32 (Fig. 6). The growth rates of fish collected in 1978 versus 1979 were significantly different ($P = 0.05$, nonparametric rank sum test). The range in average slope for the 1978 group is 0.19 to 0.25 and for the 1979 group, 0.21 to 0.32. Since the sample size was small, this test is inconclusive, but examination of the size-at-age data by year (Fig. 7) tends to support the results of the back calculations.

The influx of fish to the Moolach Beach nursery ground, determined by back calculating the date of recruitment to the sampling gear for each fish, was distributed over the winter and spring (Fig. 8). During the summer, recruitment declined and was zero by July 1978 and by September 1979.

For juveniles captured in the estuary, recruitment appeared to be concentrated over a few winter months (Fig. 9). A sharp peak is evident

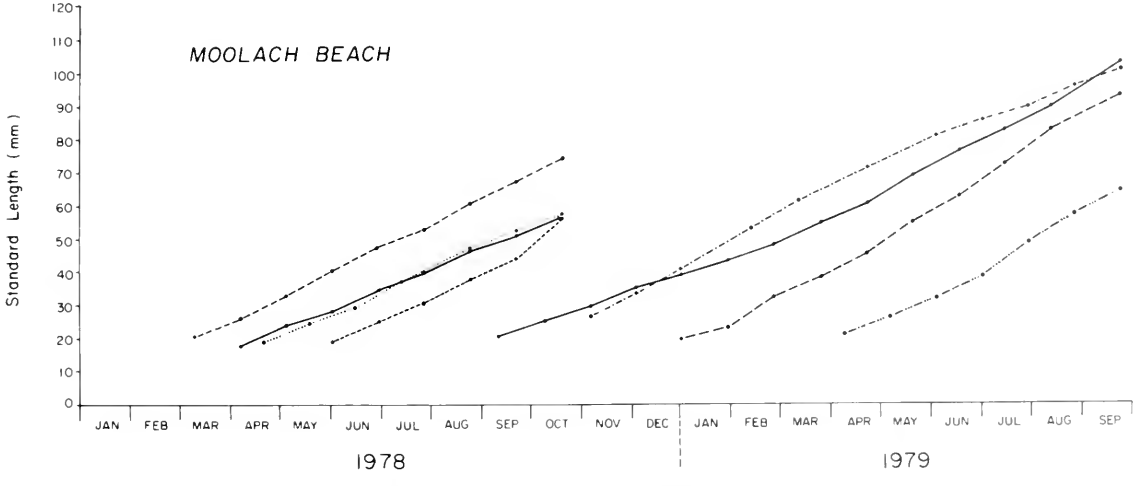

FIGURE 5.—Back-calculated growth of eight individual *Parophrys vetulus* from Moolach Beach during 1978-79.

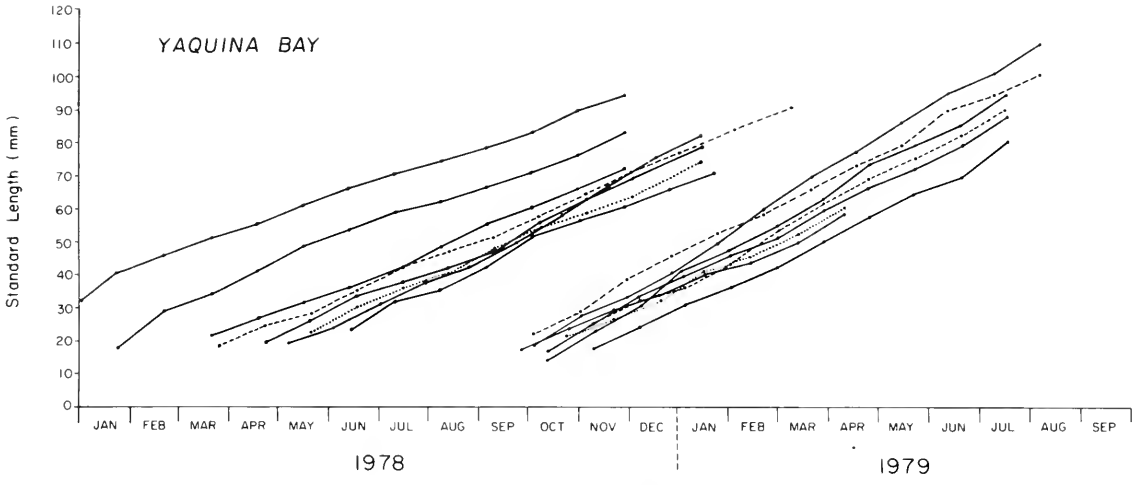

FIGURE 6.—Back-calculated growth of 16 individual *Parophrys vetulus* from Yaquina Bay during 1978-79.

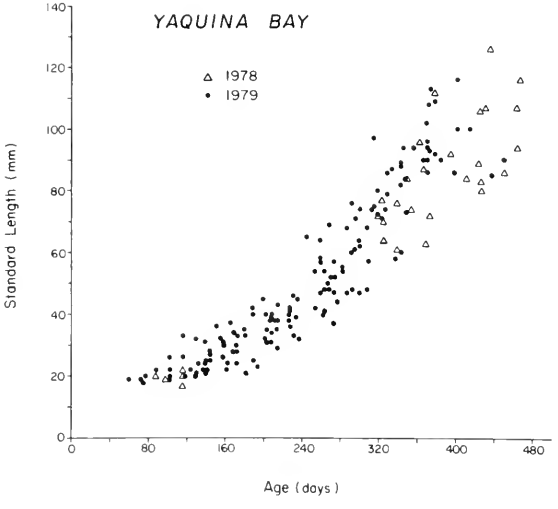

FIGURE 7.—Size-at-age data plotted by year of capture of *Parophrys vetulus*.

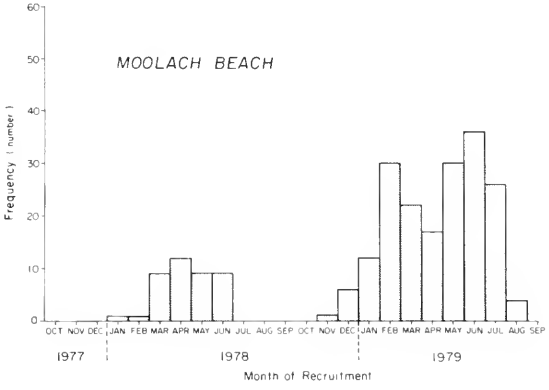

FIGURE 8.—Distribution of *Parophrys vetulus* recruitment to the sampled population at Moolach Beach during 1978-79. Full recruitment to the sampling gear was estimated to occur at 120 d of age.

in November, December, and January. As in the Moolach Beach data, recruitment goes to zero in the summer, but reappears in the fall among Yaquina Bay fish.

DISCUSSION

Several previous studies have attempted to estimate growth rates for English sole juveniles (Table 2). For the purposes of comparison with the data reported here, the total length measurements used in other studies were converted to standard length using the relationship given by Laroche and Holton (1979). The recalculated daily growth estimates from all of these other studies are similar, but are substantially higher than my estimated daily growth rates. Smith and Nitsos (1969) and Van Cleve and El-Sayed (1969) determined growth during the first year of life by back calculating the size of the fish when the first detectable annulus on the interopercular bone was formed. This occurs during the fish's first slow growth season, which may be at various ages due to the protracted spawning period of this species. Growth back calculations of individual fish (Figs. 5, 6) do not show a clear slow growth period during the first year.

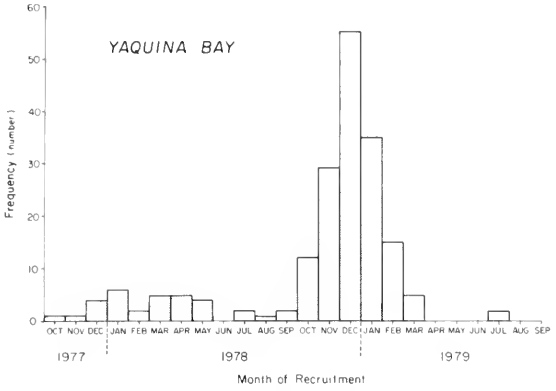

FIGURE 9.—Distribution of *Parophrys vetulus* recruitment to the sampled population in the Yaquina Bay estuary during 1978-79. Full recruitment to the sampling gear was estimated to occur at 120 d of age.

The other two studies (Westrheim 1955; Kendall 1966) utilize the technique of following modal progressions through time in length-frequency distributions. These estimates are strongly influenced by the efficiency of the sampling gear. If the smaller fish are sampled less efficiently than the larger, growth will be overestimated. Emigration of small individuals, immigration of larger fish, and differential mortality of small fish would all produce overestimates of growth using this method. Also, length-frequency modal progression may give variable results dependent on the method of choosing the modes.

Variability in the size-at-age data was much higher for fish sampled in the estuary compared with those sampled in the open coastal area, but the mean growth rates for fish from the two areas were similar. Physical factors may affect growth variability. Yaquina Bay has highly variable temperature and salinity. Frey[4] found differences of up to 5‰ salinity and 2°C between high and low tides in the lower bay. Bottom temperature in the estuary ranges between 5° and 15°C through the year, and salinity from virtually 0 to 34‰. At Moolach Beach in contrast, a more constant environment may be expected. The open coastal region does not have a large source of freshwater to influence salinity and temperature. Huyer (1977) and Huyer and Smith (1978) reported that bottom water salinity off the Oregon coast fluctuates about 1‰ from winter to summer. Temperature varies from 6.5°C in summer, due to seasonal upwelling, to about 10°C in winter.

There are two ways in which growth variability can be reduced. Either outlying individuals have their growth rates altered towards the mean or they are removed from the population. Particularly good or bad growth conditions in an area would affect the growth of all individuals, and alter the mean. Emigration and mortality are the two possible removal processes. The size-at-age plot for Moolach Beach (Fig. 3) and other data (Laroche and Holton 1979) indicate that most *P. vetulus* juveniles move out of the nearshore area at between 70 and 80 mm SL. Emigration from the estuary appears to be at a larger size, approximately 100 mm SL (Westrheim 1955; Olson and Pratt 1973).

Predation in the estuary is probably low compared with the open coast. Few large fishes are regularly found in the bay, although birds may be significant predators. Kuipers (1977), in a study of an estuarine nursery for plaice in the Wadden Sea, reported predation mortality to be low in contrast to a coastal nursery area studied by Steele and Edwards (1970).

Finally, intraspecific competition may affect growth. The estimated densities of juvenile English sole in the estuary are a consistent order of magnitude greater than at Moolach Beach (Krygier and Pearcy[5]). Competition may potentially

[4]B. Frey, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1980.

[5]E. E. Krygier and W. G. Pearcy, School of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. March 1980.

TABLE 2.—Summary of growth estimates from previous studies: the data has been recalculated so that direct comparisons can be made (see text).

Location	Size at 1 yr of age (mm SL)	Daily growth rate (mm/d)	Source
Yaquina Bay, Oreg.	117	0.40	Westrheim 1956
Monterey Bay, Calif.	108-126	0.36-0.43	Smith and Nitsos 1969
Puget Sound, Wash.	128	0.44	Van Cleve and El-Sayed 1969
Puget Sound, Wash.	—	winter 0.48 summer 0.73	Kendall 1966

emphasize differences among individuals and increase observed variability.

The most plausible mechanism for explaining low growth variability at Moolach Beach combines limitation and removal processes. If the population is food limited in the open ocean and selective predation on smaller, slower growing individuals is occurring, the observed variability in size-at-age will be small. Using the otolith aging technique this hypothesis is testable. It requires a comparison of the size-at-age distribution of fish found in the stomachs of predators with the distribution shown in Figure 3.

A hypothesis arising from this study is that survival, not growth, is enhanced in the estuarine nursery ground compared with the open coast. Testing of this hypothesis will be an important step in understanding the role that estuaries play in the life history of many fishes.

ACKNOWLEDGMENTS

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POPULATION FLUCTUATIONS OF CALIFORNIA SEA LIONS AND THE PACIFIC WHITING FISHERY OFF CENTRAL CALIFORNIA[1]

DAVID G. AINLEY, HARRIET R. HUBER,[2] AND KEVIN M. BAILEY[3]

ABSTRACT

Seasonal fluctuations in the number, age ratios, and diet of California sea lions, *Zalophus californianus*, were studied at the Farallon Islands, central California, from 1971 to 1980. During these years, average monthly numbers increased geometrically, except for April and May. Before 1977, the annual peak in population occurred during April and May, almost no animals were present late June to early July, and a slight peak occurred during fall; adult males predominated. Beginning in 1977, fall numbers equaled or exceeded those in spring, large numbers remained throughout summer, and subadults predominated. We hypothesize that seasonal fluctuations in sea lion numbers were related to the availability of their principal prey, Pacific whiting, *Merluccius productus*, and that the changes that began in 1977 were related to termination of the whiting fishery off central California beginning that year.

The California sea lion, *Zalophus californianus*, ranges along the North American west coast from the Gulf of California to British Columbia. Bartholomew (1967) hypothesized that most adult males migrate to the north from breeding sites in Baja California and southern California beginning in midsummer and remain there until the early spring when they return south, and that females and young animals remain in the vicinity of breeding areas or move somewhat southward during the nonbreeding season. This has become the accepted explanation to account for the seasonal movements in the population (e.g., Mate 1975). Preliminary analysis of census and diet information collected at the Farallon Islands during 1971-80 led to a related hypothesis that the movements of male sea lions toward the north could be a response to the seasonal occurrence and availability of an important prey species, the Pacific whiting, *Merluccius productus* (Huber et al.[4]). This information was later quoted by Fiscus (1979). Additional analysis, presented here, provides more insight into the ecological relationship between the two species.

The Pacific whiting is an abundant midwater fish of the continental slope and shelf off California. A summary of its biology and of the whiting fishery is provided by Dark (1975), Fiscus (1979), and Dark et al. (1980). Pertinent to the present study are the fish's migrational patterns. Pacific whiting migrate vertically from near bottom in daytime towards the surface at night, except in the winter spawning season when they remain at depth. They spawn off the coast from Baja California to central California and migrate northwards in spring and summer to feed off the Oregon, Washington, and British Columbia coasts. Small adults and juveniles migrate a lesser distance—1 to 3-yr-olds are mainly located off central and southern California from spring through fall. Also pertinent is the major harvest of whiting conducted by eastern European trawlers off the Pacific coast states and Canada from 1966 to 1976. Much of the fishing was concentrated in the Farallon area. Under the Fishery Conservation and Management Act of 1976 (FCMA), the fishery was prohibited off central California (south of lat. 39°N); we hypothesize that termination of the fishery affected the occurrence of California sea lions and possibly other pinnipeds.

METHODS

California sea lions were counted at the south Farallon Islands (lat. 37°42'N, long. 123°00'W), which are situated at the continental shelf break 32 km offshore from Point Reyes and Bolinas Point, Calif. Counts were irregular but fairly frequent from 1971 through 1973, but were regu-

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[4]Huber, H. R., D. G. Ainley, S. Morrell, R. R. LeValley, and C. S. Strong. 1979. Studies of marine mammals at the Farallon Islands, California, 1977-78. Final rep., 50 p. Marine Mammal Commission, Wash., D.C.; available Natl. Tech. Inf. Serv., Springfield, VA 22151, as PB80-111602.

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FISHERY BULLETIN: VOL. 80, NO. 2, 1982.

lar and weekly during following years to January 1980. They were made year-round and occurred after 1400 h when maximum numbers of sea lions haul out at Southeast Farallon (Fig. 1; see also Mate 1975). In the following analyses the 1971-73 censuses were combined (Fig. 2) to correct for sporadic coverage. During censuses in the last 9 mo of both 1975 and 1976, and in all censuses since, animals were differentiated into adults and subadults, virtually all of which were males. Total count results are presented in Huber et al. (footnote 4).

Whiting otoliths and squid beaks were collected at regular biweekly intervals from the boat dock at North Landing, Southeast Farallon Island. This is a favored haul out site for California sea lions but not for other pinnipeds. Whiting otolith radii were measured and prey length was determined from the relationship of fish length to otolith radius. We assume that significant dissolution of otoliths did not occur as a result of digestion. Prey totals were determined by dividing otoliths by two and taking the higher number of upper and lower squid beaks.

Counts of trawlers fishing for whiting were made by the Division of Enforcement and Surveillance, National Marine Fisheries Service. Catch statistics were made available by the Northwest and Alaska Fisheries Center, NMFS.

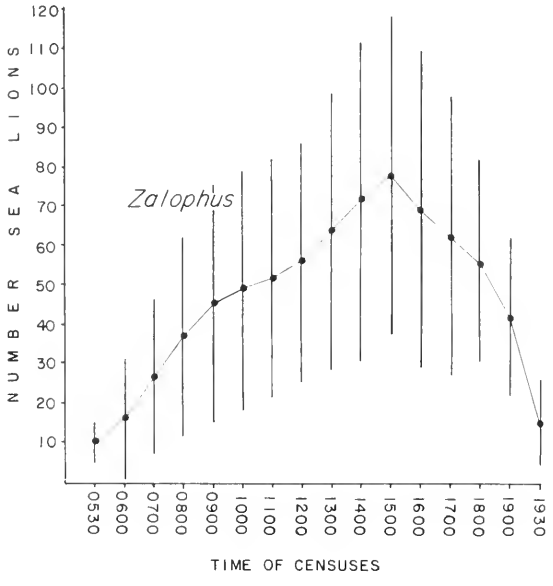

FIGURE 1.—The number of California sea lions hauled out during hourly periods at Shubrick Point, Southeast Farallon Island; the mean and ± standard deviation are shown based on 12 all-day watches during April and May 1974.

RESULTS AND DISCUSSION

California Sea Lion Biology

Aside from the one pup born at Southeast Farallon, every year since 1974 except 1978 (plus its mother and at least one bull) (Pierotti et al. 1977; Huber et al. [footnote 4]; Point Reyes Bird Observatory unpubl. data), the California sea lion population was comprised of nonbreeding males. Major breeding sites are located in the southern California islands (Bartholomew 1967; LeBoeuf and Bonnell 1980). From 1971 to 1976 a large peak in numbers was reached each year at the Farallones in late April or early May, when animals migrating south toward southern breeding sites hauled out for short periods (Fig. 2). A majority of animals departed (temporarily?) each evening to feed (Hobson 1966); about an hour after dawn they began to return and by early afternoon maximum numbers were hauled out. Numbers present each day rapidly declined in late May, and by late June only a few *Zalophus* hauled out. Population size increased again in late July, reached a peak in August or September that was much smaller than in spring, and than declined to a level maintained through the

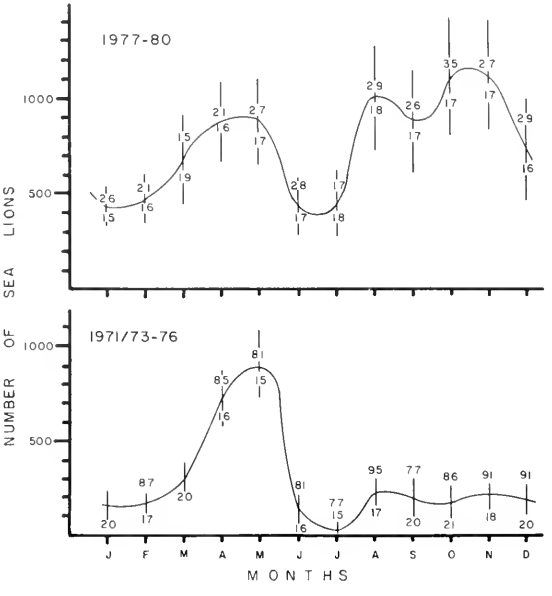

FIGURE 2.—The mean (± standard deviation) number of California sea lions hauled out at Southeast Farallon Island each month during two periods: 1971/73-76 and 1977-80; below each curve are the number of censuses each month and above are the proportion of adults present.

winter. Average monthly population size increased slightly from one year to another (Fig. 3). The proportion of adults present each month ranged between 73 and 95%.

Since 1977, population fluctuations of the California sea lions have been markedly different in several ways. First, except for April and May, average monthly population size began to increase rapidly from one year to the next (Fig. 3). This was especially evident for the summer and fall and thus, secondly, by 1978 the timing of the annual maximum population had shifted and fall counts were exceeding those of the spring peak (Fig. 2). In fact, for each month except April and May, average monthly numbers increased geometrically from 1971-73 to 1980 (least squares; r ranged 0.7745 to 0.9537, $P<0.01$). Finally, the percentage of adults during 1977-80 was reduced to a range between 15 and 35%. These differed significantly from percentages of adults in the period 1971/73-76 ($P<0.01$; percentage test, Sokal and Rohlf 1969:608). Young animals were thus migrating north rather than remaining in southern California and Baja California waters as Bartholomew (1967) had noted in earlier years.

Seasonal population fluctuations and age ratios at the Farallones from 1971 to 1976 were largely similar to those at coastal sites, as measured at Año Nuevo Island (80 km away, Orr and Poulter 1965; Lance and Peterson 1968), and sites farther north (Mate 1975). Exceptional at the Farallones was the fact that there was almost no fall peak, whereas at coastal sites it greatly exceeded the peak in spring. When the fall peak increased in 1977 the Farallon pattern became similar to coastal sites. However, it is possible that the age composition, for which few comparative data are available, and the size of the spring peak were changing then at the Farallons. At coastal sites there is a small spring peak and a large fall peak, but at the Farallones the two peaks became equal in magnitude.

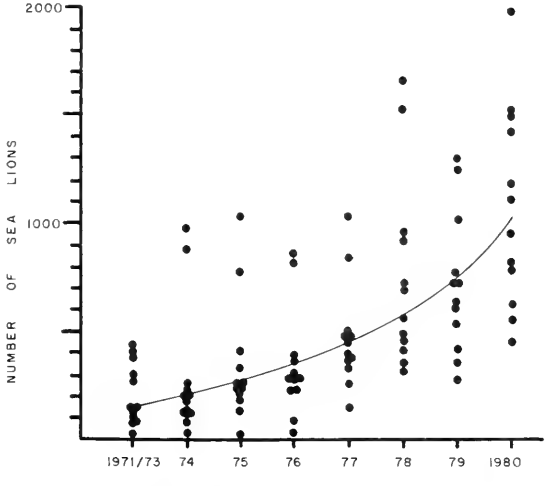

FIGURE 3.—The average number of California sea lions hauled out annually at Southeast Farallon Island. Dots above each year are monthly averages; the curve is described by the geometric equation: $y = a\lambda^x$, where $a = 9.5 \times 10^{-8}$ and $\lambda = e^{0.2979}$; $r = 0.6557$, $P<0.01$.

The diet of California sea lions at the Farallones, as revealed by regurgitated items, has been comprised of at least 20 species of prey (Table 1) (some otoliths could actually have come from the stomachs of sea lion prey). Outstanding were the predominance of Pacific whiting, particularly from April to August, and the diversification in diet from September to March. The whiting eaten averaged 25 to 36 cm in length and were 2 to 3 yr of age (Bailey and Ainley in press). Except for the short period during summer when they were away at breeding sites, California sea lions were most abundant when whiting predominated in their diet. At coastal sites of central California, the market squid, *Loligo opalescens*, along with whiting and northern anchovies, *Engraulis mordax*, are dominant prey of this pinniped (Morejohn et al. 1978).

California Sea Lions and the Pacific Whiting Fishery

From 1967 to 1972 most Pacific whiting were caught off the coasts of British Columbia, Washington, and Oregon (Fig. 4). After 1972, catches increased off the California coast, and especially high catches of around 100,000 t occurred from 1974 to 1976. This southward shift of fishing is believed to be due to a depletion of large adults in the Pacific Northwest. Fishing off central California targeted juvenile whiting.[5] After the FCMA restriction on fishing south of lat. 39°N, the total whiting catch dropped significantly (Fig. 4).

Whiting prevalence in the diet of Farallon sea lions was directly correlated to the average monthly number of trawlers fishing for whiting in the Farallon area (Table 2; $r = 0.747$, $t = 3.55$,

[5]Anonymous. 1976. Summary of National Marine Fisheries Service views on the status of the Pacific hake resource. Unpubl. rep., 4 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, 2725 Montlake Blvd. E., Seattle, WA 98115.

TABLE 1.—Percent composition of California sea lion diet as determined by otoliths and beaks regurgitated at haul out sites, Southeast Farallon Island, 1974-78.

Months:	J	F	M	A	M	J	J	A	S	O	N	D
Cephalopods												
Octopus rubescens		1	2									
Berryteuthis (?) sp.									1			
Gonatus sp.				1								
Loligo opalescens									3			
Fishes												
Merluccius productus	54	36	28	87	94	98	96	84	38	43	28	30
Sebastes spp.	45	27	61	11	5	<1		14	30	16	69	30
Porichthys notatus		1	6	1	1	<1		<1	1	31	1	
Engraulis mordax		20						<1				1
Glyptocephalus zachirus	1					<1			10	1	1	40
Chilara taylori		8				<1			9			
Parophrys vetulus		2						<1	3			
Genyonemus lineatus						<1		<1	2	2		
Citharichthys sordidus		1							2	3		
Microgadus proximus		1	2					<1	<1			
Atherinopsis californiensis								<1	<1			
Leptocottus armatus									<1	2		
Zalembius rosaceus									<1	2		
Microstomus pacificus									<1			
Trachurus symmetricus							4	<1	<1			
Clupea pallasi								<1				
Lyopsetta exilis									<1			
Total prey (no.)	11	147	55	550	1,077	291	45	535	267	102	140	10

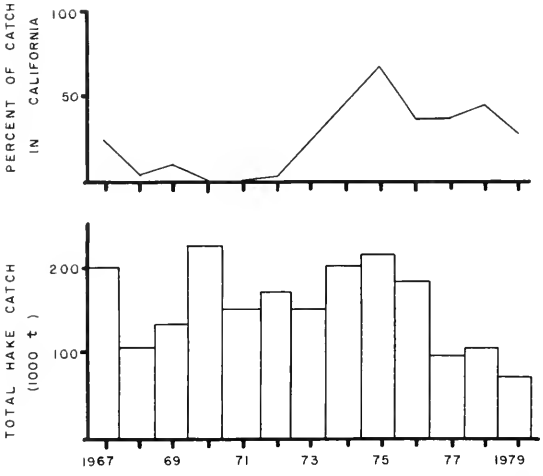

FIGURE 4.—The total catch of whiting in the Pacific coast fishery and the proportion of that catch taken off California, 1967-79.

TABLE 2.—Number of stern trawlers fishing for Pacific whiting over the California continental slope between lat. 39° and 37°N from January through December 1974-77; data summarized from NMFS monthly surveillance reports.

Year	J	F	M	A	M	J	J	A	S	O	N	D
1974	0	0	13	43	55	60	57	55	11	0	0	0
1975	3	8	60	64	90	64	2	?	0	0	0	0
1976	0	0	10	35	55	50	38	13	0	0	0	0
1977	0	0	0	0	0	0	0	0	0	0	0	0
$\bar{x}$ 1974/76	1	2	28	47	67	58	32	34	3	0	0	0

df = 10, $P<0.01$, Spearman rank correlation). Considering the whole coast of California, trawlers concentrated near the Farallones, at least from 1974 to 1976, when fishery surveillance records were available to us. If we assume that the number of trawlers and the prevalence of whiting in sea lion diets, in conjunction with sea lion population size, reflect whiting availability, we conclude that both sea lions and humans were attracted to continental slope waters at the same time in order to catch whiting. The only difference was that the sea lions departed at the peak of harvest in order to return to traditional breeding sites.

Associated with the unavailability of whiting, both fishing activity and the preponderance of whiting in the sea lion diet dropped off from September to March. During the winter months adult whiting migrate off the continental shelf to spawn in deeper waters of the continental slope (Bailey 1980), and juveniles probably show the same behavior. In addition, during the spawning months they do not diurnally migrate but remain deep (Nelson and Larkins 1970). They are thus unavailable to both the fishery and the sea lions.

We offer the following hypothesis to explain the patterns observed in the sea lions' behavior. First, they are attracted to continental slope waters of central California by whiting which, due to their own migrations, become available there during spring and summer. The trawler fishery, also attracted by greater fish availability, was perhaps depleting whiting stocks seasonally to such an extent during the early to mid-1970's that by late summer when sea lions were

returning north from breeding sites, offshore waters near the Farallones were no longer as attractive to the pinnipeds as during the spring. The sea lions thus remained along the coast to feed on other prey. Then in 1977, when trawlers no longer fished for whiting off central California, the sea lions responded in three ways, all possibly due to increased food supply during summer and fall: 1) Young animals moved farther north or farther off the coast than previously, 2) more adults remained during summer instead of migrating south, and 3) adults returning from southern breeding sites moved offshore in larger numbers than they had in previous falls. The size of the sea lion population peak during spring was not affected by termination of the fishery, because fishing was only just getting under way each year at that time.

Adding coincidental support to the hypothesis that the 1966/76 whiting fishery off central California was indirectly depressing the numbers of California sea lions in the vicinity are data from other localities. Populations of California sea lions at breeding sites on southern California islands have been increasing geometrically for the past several decades (Bartholomew 1967; LeBoeuf and Bonnell 1980; LeBoeuf[6]). At the crease in numbers at the Farallon Islands is likely a reflection of this. Successive counts at coastal Año Nuevo Island during the early 1960's also reflected this increase, but beginning sometime between 1963 and 1967 numbers began a decline there that lasted through 1975; since then, however, they have begun to increase again (LeBoeuf and Bonnell 1980; LeBoeuf[6]). At the Monterey breakwater, about 80 km farther south, D. J. Miller[7] has noted that numbers of subadult California sea lions since about 1978 have been much higher than in previous years.

Changes in the occurrence of another pinniped, the northern fur seal, *Callorhinus ursinus*, at the Farallones, provide additional support to the hypothesis. Also an important whiting predator (Fiscus 1979), this species breeds at San Miguel Island in southern California and in the Bering Sea, and during the nonbreeding season frequents waters of the California continental slope. From 1970 to 1976 we observed individual fur seals at the farallones on only 3 single days, each 2 yr apart. Since then, however, their occurrence has changed dramatically: the species has occurred annually during the summer and fall, and at least 10 different individuals (determined by tags or peculiar scars) have hauled out, some repeatedly, for periods of variable length. Two that hauled out were tagged at San Miguel; another has hauled out for 5 yr in succession. The fur seal breeding population on San Miguel Island has been increasing geometrically from the early 1960's to the present (LeBoeuf and Bonnell 1980) and the increasing occurrence of this species on the Farallones is likely a reflection of this trend. The dramatic jump in numbers at the Farallones beginning after 1976, however, is out of line with the continuous increase in breeding numbers. Cessation of the whiting fishery off central California in 1976 may account for the change at the Farallones, just as this may be responsible for the change in population dynamics of California sea lions in central California.

[6]B. J. LeBoeuf, Division of Natural Sciences, University of California at Santa Cruz, Santa Cruz, CA 95064, pers. commun. June 1981.

[7]D. J. Miller, California Department of Fish and Game, Monterey, CA 93940, pers. commun. June 1981.

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FEEDING BEHAVIOR OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, IN THE WESTERN NORTH ATLANTIC

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ABSTRACT

Observations on the feeding behavior of the humpback whale, *Megaptera novaeangliae*, were made from aerial and surface platforms from 1977 to 1980 in the continental shelf waters of the northeastern United States. The resulting catalog of behaviors includes two principal categories: Swimming/lunging behaviors and bubbling behaviors. A behavior from a given category may be used independently or in association with others, and by individual or groups of humpbacks.

The first category includes surface lunging, circular swimming/thrashing, and the "inside loop" behavior. In the second category, a wide variety of feeding-associated bubbling behaviors are described, some for the first time. The structures formed by underwater exhalations are of two major types: 1) bubble cloud—a single, relatively large (4-7 m diameter), dome-shaped cloud formed of small, uniformly sized bubbles; and 2) bubble column—a smaller (1-1.5 m diameter) structure composed of larger, randomly sized bubbles, used in series or multiples. Both basic structures are employed in a variety of ways.

Many of these behaviors are believed to be utilized to maintain naturally occurring concentrations of prey, which have been identified as the American sand lance, *Ammodytes americanus*, and occasionally as herring, *Clupea harengus*.

This paper reports on the feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the continental shelf waters of the northeastern United States. We describe several feeding behaviors reported for the first time, as well as a number of behaviors known from other areas but not previously reported for these waters. Our collective observations provide the beginning of a more complete catalog than has previously been available.

Early observations of humpback feeding behavior were made by Ingebrigtsen (1929) from the Norwegian Sea near Bear Island:

> "It [the humpback] employed two methods of capturing 'krill' when the latter was on the surface of the water. One was to lie on its side on the surface and swim round in a circle at great speed, while it lashed the sea into a foam with flukes and tail and so formed a ring of foam. The frightened 'krill' gathered together in the circle. This done the humpback dived under the foam-ring and a moment later came up in the center to fill its open mouth with 'krill' and water, after which it lay on its side, closed its mouth, and the catch was completed.
>
> "The other method was to go a short distance below the surface of the water, swimming in a ring while at the same time it blew off. The air rose to the surface like a thick wall of air bubbles and these formed the 'net'. The 'krill' saw this well of air bubbles, were frightened into the centre, and then the manoeuvre of the first method was repeated."

Some 45 yr later, "bubblenetting" was reported from Alaskan humpbacks by Jurasz and Jurasz (1978), and later described in detail (Jurasz and Jurasz 1979). With the exception of the work of Watkins and Schevill (1979), accounts of feeding behavior of this species in the waters of the western North Atlantic are few and largely anecdotal.

MATERIALS AND METHODS

Observations were made from dedicated aircraft (a Cessna 337 Skymaster and a Beechcraft AT-11[4]), from dedicated surface vessels (the 27.5 m *Dolphin III* and the 21.3 m *Tioga*), from platforms-of-opportunity, and from shore stations.

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

All data were collected by experienced observers. Photographs taken in both 35 mm and 70 mm format documented most observations, and were supplemented by written and occasionally tape-recorded field notes. From the aircraft, observers estimated the critical dimensions of feeding-associated structures with respect to references such as the whale's body or flipper length. From shipboard, more precise measurements were obtained through reference to known dimensions on the vessel, or to a 25 cm diameter fiberboard disk which had been deployed in the immediate vicinity of the whale.

RESULTS

Feeding behaviors were observed on more than 150 occasions in the period April 1977 to May 1980. Observations were made in the area of West Quoddy Head, Mt. Desert Rock, Stellwagen Bank, the waters east and southeast of Cape Cod, and southeast of Block Island (Fig. 1). Feeding, or apparent feeding, was reported for individuals and for groups of up to 20 whales.

Behaviors

Circular Swimming/Thrashing

On 2 December 1978, a single humpback whale was observed and photographed swimming in a broad (23 m) circle, roiling the surface as it swam. Tail slashing (a rapid sideways sweeping of the flukes) may have accompanied this behavior. Dense flocks of birds were present over the whale, and dolphins were present by the head and body. The presence of both of these feeding-associated elements, as well as the resemblance to observations by Ingebrigtsen (1929), suggested that feeding was taking place.

This initial observation was substantiated in May 1980 when a number of shipboard observations confirmed the behavior as feeding associated. An initial thrust of the flukes was followed by the whale's swimming in a broad circle, roiling the surface with flippers and flukes. This was followed in many, but not all, cases by a feeding rush through the circle. This behavior was repeated many times by a single animal over a period of several hours.

The circular swimming/thrashing behavior, observed on two occasions, each time involving a single whale, is considered relatively uncommon.

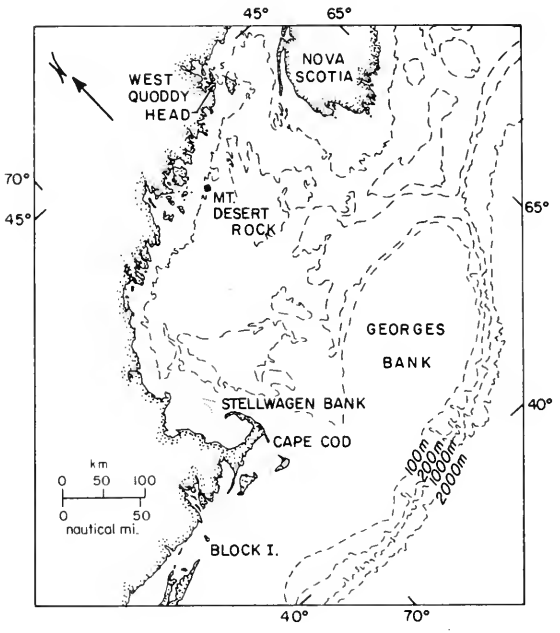

FIGURE 1.—Study area where observations of feeding behaviors were made. Place names on chart are those referred to in text.

Lunge Feeding

Lunge feeding is defined as an upward rush at the water surface with the longitudinal axis of the body intersecting the plane of the surface at an angle of 30°-90°. As the whale breaks the surface, the mouth is agape, and quite often a greatly distended throat region is seen. Up to one-third of the body length clears the surface before the whale falls or settles back into the water. Observations and photographs of prey at the surface, in the mouths of the whales, and picked up by closely associated birds leave no doubt that this is a capture mode of feeding behavior. This common behavior has been recorded in 21% of our feeding observations, from single animals as well as from groups. When several animals fed together, the lunges often were simultaneous and in close proximity (3 m). In several cases, two or more animals came in contact, bumping each other as they lunged. Bouts of lunge feeding may contain on the order of 20 lunges (3 animals in one case) in 25 min.

The speed at which the lunge takes place is highly variable. At times, the whale bursts through the surface in a vigorous upward rush. At other times, the rise to the surface and the subsequent extension of the rostrum and dis-

tended lower jaw above the surface are quite gradual. In several instances, humpbacks were observed feeding in this manner (the slow, gradual rise) in formation. Five or six whales arranged side by side and slightly staggered of one another acted in unison. This behavior has been similarly described from Alaskan waters and termed "echeloned" lunge feeding (Jurasz and Jurasz 1979).

Inside Loop Behavior

On 23 May 1980, a single humpback was observed feeding for over 1 h. The whale repeatedly displayed a behavior we have termed an "inside loop." As the whale begins a shallow dive, it sharply strikes the water's surface with its flukes. This action creates an area of turbulence in the water estimated to have an average diameter of 9 m. This area of foam and bubbles is seen clearly as the whale swims away at a shallow dive angle with the pectoral fins held horizontally. The whale, swimming rapidly, then rolls 180°, so that the white ventral surface of the flukes can be seen just below the surface. An inside loop (a sharp U-turn in the vertical plane) follows immediately, so that the whale is now swimming toward the area of turbulence. Finally, the whale is seen rising vertically in a slow lunge, with mouth widely agape, through the center of the turbulence created by the fluke slap. The horizontal distance covered by this "out-and-back" motion was on the order of 1½-2 body lengths of the whale. The behavioral sequence is illustrated diagrammatically in Figure 2.

Several variations on the basic behavior were observed. The humpback did not feed through the area of turbulence in every instance. Occasionally, the whale would surface to the side of the disturbance, not always feeding. On other occasions, a second whale would enter the general area and subsequently be seen lunge feeding through the disturbance created by the flukes of the first whale, either alone or in unison with the original whale.

The inside loop behavior, observed on a single occasion, involving a single whale later joined by a second, is at present considered relatively uncommon.

Bubbling Behaviors

Underwater exhalations or bubbling behaviors were seen in association with feeding, or apparent feeding, in 52% of our feeding observations. These exhalations appear to be of two major types, forming what we have termed "bubble columns" and "bubble clouds." In general, bubble columns and bubble clouds have been observed with about equal frequency.

BUBBLE COLUMNS.—Bubble columns are formed by the underwater exhalations of a whale swimming from 3 to 5 m (estimated) below the surface. As the bubble bursts are released, they rise vertically to the surface in the form of a somewhat ragged column. The columns are 1-2 m in diameter and are composed of random-sized bubbles estimated to be generally >2 cm. Series of from 4 to 15 bubble columns are used to form rows, semicircles, and complete circles or bubble nets (Figs. 3, 4).

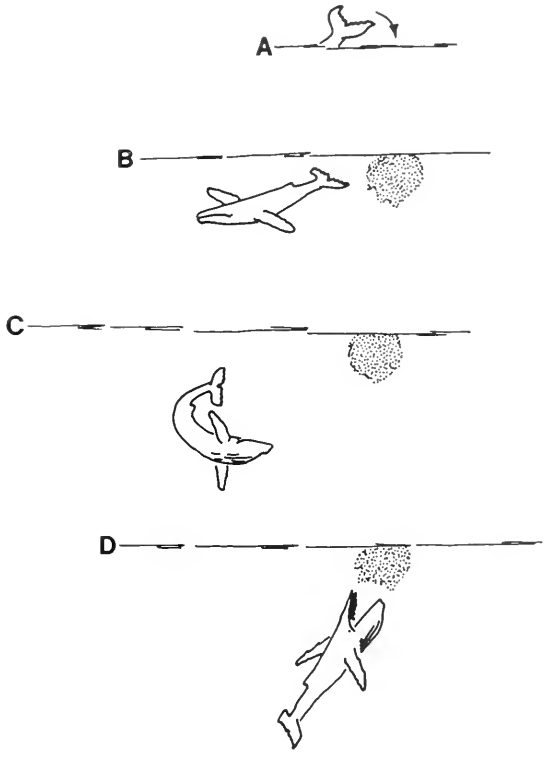

FIGURE 2.—"Inside loop" type of feeding behavior. A. Upon making a shallow dive, humpback whale strikes the surface sharply with flukes. B. Fluke slap creates an area of turbulence (foam/bubbles) as whale swims away in a shallow dive, flippers held horizontally. C. Whale executes a 180° roll and now does a sharp inside loop, or U-turn in the vertical plane. D. Whale lunge feeds through the area of disturbance created by original fluke slap.

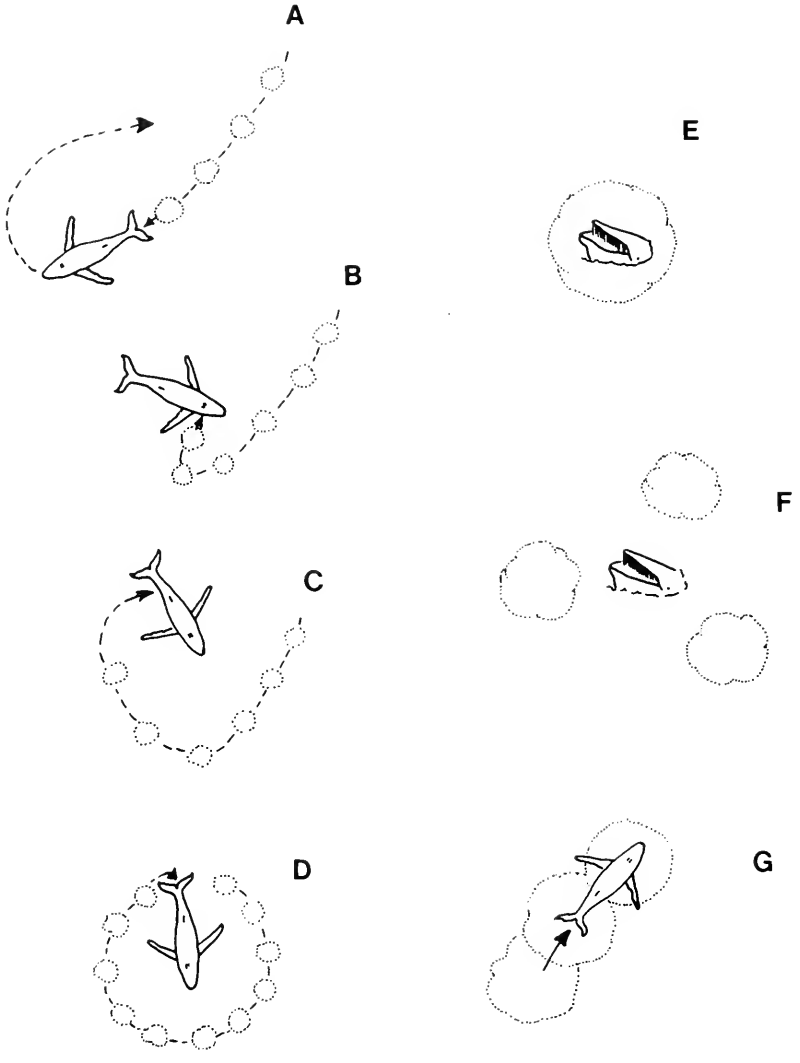

FIGURE 3.—The seven types of bubbling behaviors associated with feeding in humpbacks. A through D are structures using bubble columns, which are 1-1½ m in diameter and composed of nonuniform-sized bubbles (estimated at >2 cm). E through G are bubble cloud structures, 4-7 m in diameter, and composed of uniform-sized bubbles (estimated at <2 cm). A. Bubble row. B. Bubble row with "crook," whale feeding location shown. C. V or semicircle shaped bubble curtain. Whale feeds in and through open side of the semicircle. D. Complete circular formation, or bubble net. E. Single bubble cloud. In this example, one of several variations, whale lunge feeds through center. F. Triangular formation of multiple bubble clouds. G. Linear formation of multiple bubble clouds.

In the simplest configuration, bubble rows, the whale creates a line of columns (generally 4-6). When this has been completed, the whale turns sharply and feeds, open-mouthed, either at or below the surface, at an acute angle to the screen formed by the row of bubble columns. In some cases, the whale continues to release bubble bursts during its turn, so that the line of bubble columns has a "crook" in the end where the whale feeds. The behavior associated with a semicircle of bubble columns is similar, in that once a semicircle (or "V") has been constructed, the whale appears and feeds toward the concave portion of the screen.

Complete circles of bubble columns, termed bubble nets (Jurasz and Jurasz 1979), have been

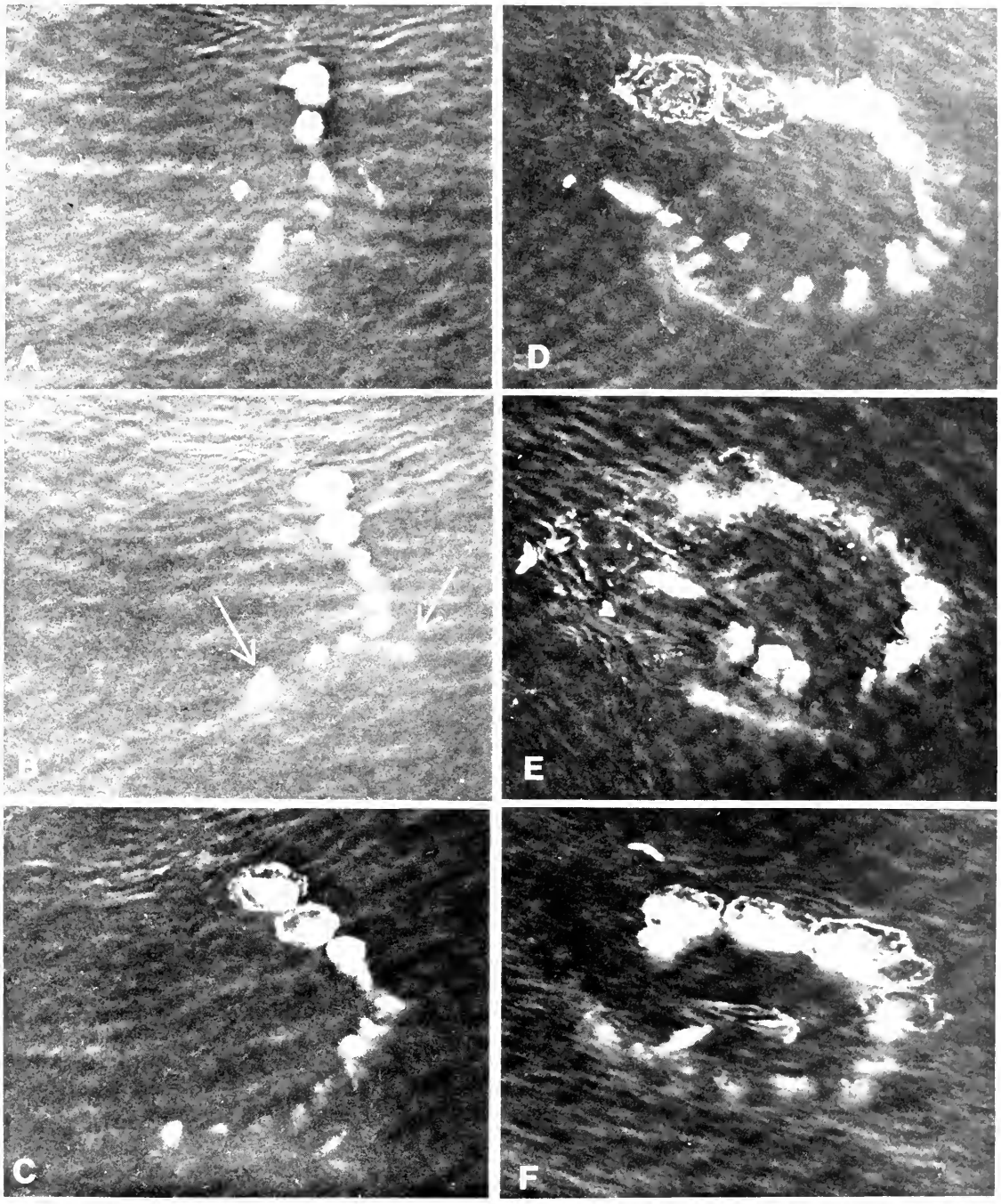

FIGURE 4.—Aerial views of bubble net construction by a humpback whale. A through E are 5 frames from a 29-frame sequence; F is from a sequence immediately following. Underwater exhalations are used to form a bubble net approximately 15 m in diameter, composed of some 15 individual bubble columns. Arrows in B indicate undersides of left pectoral fin and flukes. In A through C, whale is rotated on its longitudinal axis so that the blowhole and dorsal surface are toward the center of the circle. In D, whale turns sharply about on the right pectoral fin and prepares to pass through the center of the net. A stream of turbulence is seen trailing from the dorsal fin area, which is being sharply thrust to the whale's left. In E, the whale is seen in feeding posture, mouth agape, underwater in the center of the net. In F, the whale surfaces and blows weakly before exiting the area of the net. Photographs by S. Kraus.

seen on a relatively few occasions, approximately 8% of our observations. Our clearest observations have been from aircraft, particularly on 23 April 1979 when several sequences of bubble net formation were photographed (Fig. 4). The whale, maintaining its longitudinal body axis on a nearly horizontal plane, swims some 3-5 m (estimated) below the surface in a circular pattern. The dorsal surface (and blowhole) of the whale is rotated toward the center of the circle so that the flippers are oriented nearly in the vertical plane. As the whale swims in this manner, approximately 15 bubble bursts are released, which rise to the surface as columns and appear to form an effective corral. As the circle or net nears completion, the whale appears to pivot on the axis of the flippers. The flukes are thrust to the outside, and a stream of underwater turbulence is seen trailing from the region of the dorsal fin. The whale then banks to the inside and turns sharply into and through the center of the net—all below the surface of the water. The aerial photographs show apparent feeding, i.e., the mouth is agape and the lower jaw region is greatly distended. Only after this stage does the whale rise to the surface, pause, and blow one or more times before exiting the area of the bubble net. Measurements show the circle to be approximately equal in diameter to the whale's length—about 13-15 m. While bubble nets constructed in both the clockwise and counterclockwise directions have been observed, the clockwise direction appears to be more common.

There are several variations to the behavior described above. Shipboard observations in May 1980 showed that bubble nets are not restricted to 360° circles, but instead may include from 1¼-2 complete revolutions as the whale swims in a spiral of decreasing radius. Often, smaller bursts of smaller bubbles made up the greater portion of the outer ring, with the bursts and bubbles both increasing in size within the inner ring. Additionally, a line of bubbles 10-30 m in length would often directly precede the formation of the circular portion of the bubble net. This gave the overall structure the shape of a "6" or a "9." Finally, surface lunge feeding (gradual rise type), rather than underwater feeding, was reported from this series of shipboard observations.

BUBBLE CLOUDS.—Bubble clouds form the second major category of bubbling behaviors associated with feeding. There are several marked differences to the bubble columns described above. In this case, a single underwater exhalation forms a single, relatively large (4-7 m diameter), dome-shaped "cloud" made up of small (estimated to be <2 cm), uniformly sized individual bubbles (Fig. 5). In a few observations where we were able to see the early stages of bubble cloud formation, the cloud appeared quite narrow initially, about 2-3 m in diameter, but expanded as it rose toward the surface. In many observations, schools of American sand lance, *Ammodytes americanus*, were visible over wide areas in patches at the surface in the general area of feeding activity, but prior to the onset of any bubbling behavior in their immediate vicinity. In all observations, the whale dove out of sight to produce the bubble cloud which rose gradually toward the surface. The prey, appearing as a disturbance at the surface, would at times leap vigorously into the air when the bubble cloud surfaced into the school.

The subsequent appearance of the whale relative to the bubble cloud displayed a good deal of variation. Observations to date suggest five possible variations, as illustrated in Figure 6. When lunge feeding through the cloud's center was seen (Fig. 6A), the speed of the lunge was slower than lunge feeding observed in the absence of clouds. In the second type of behavioral sequence (Fig. 6B, the slow, horizontal appearance of the whale in the surfaced cloud), over 70 bubble cloud observations recorded from shipboard in 1978-79 suggest a repetitive, rigidly patterned activity composed of the following:

1) The whale sounds, usually with flukes in the air.

2) A cloud of bubbles appears beneath the sea surface up to 2½-3½ min after sounding.

3) The whale, not obviously swimming, rises slowly to the surface. Its back first appears in the center of the spent cloud of bubbles 5-9 s after the first bubbles in the cloud reach the surface.

4) Three to ten blows and slow, shallow diving precede the sounding dive which begins the next sequence.

In this common activity, the actual feeding probably takes place in the cloud and below the surface, with the whale's appearance marking the conclusion of the episode. Although no feeding is visible at the surface, the presence of a number of important elements (prey abundant in bubble clouds, similarity of structure to those in known

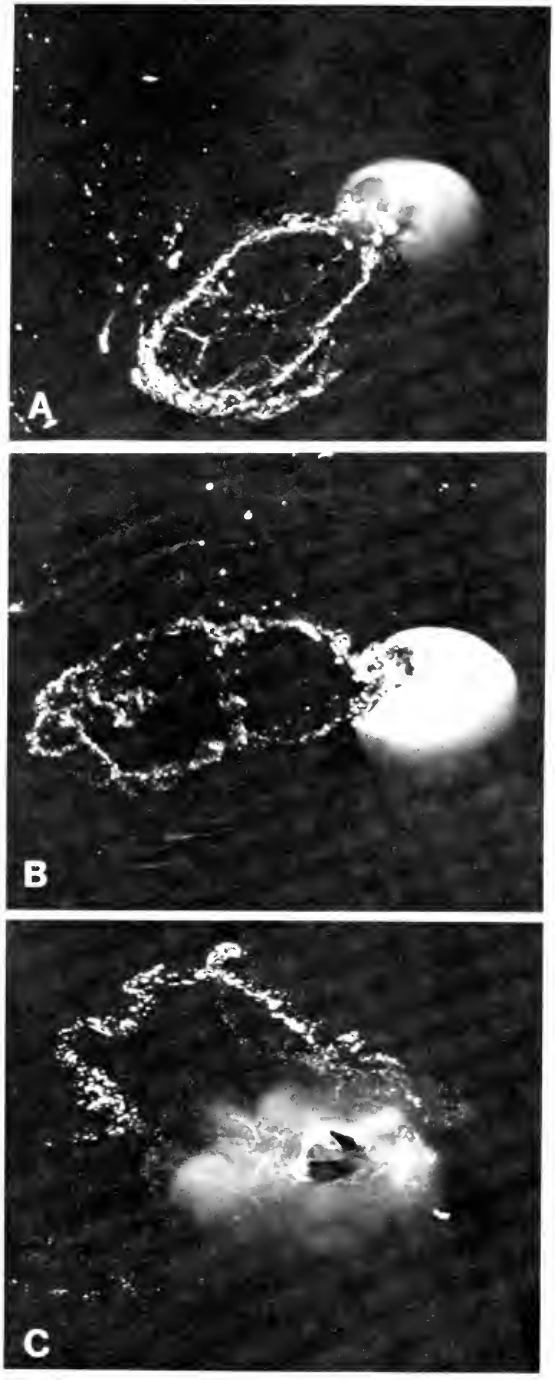

FIGURE 5.—Aerial views of bubble cloud formation and associated feeding. A. Dome-shaped bubble cloud, formed by underwater exhalation, seen rising toward surface. B. Bubble cloud after intercepting plane of surface—upper portion of structure is flattened. C. Lunge-feeding whale appears through center of bubble cloud. Photographs by A. Frothingham.

feeding events, repeated occurrence in known feeding areas, and the presence of feeding birds) is strongly suggestive of a feeding-associated behavior.

Bubble clouds were also observed being used in series or multiples. These clouds possess the characteristics described above but are used in groups, generally three, by one or more humpbacks. Two varieties have been seen (Fig. 3F, G): 1) individuals or groups of humpbacks blow clouds in either triangular or random patterns, and feed in the midst of the clouds or within a particular cloud—observed on a number of occasions and considered relatively common; and 2) an individual whale was seen to blow three linearly connected clouds, and then swim on the surface very slowly through the formation—observed on a single occasion and considered uncommon.

A final variation, which may or may not be directly associated with feeding, is poorly understood. At times, a lunge-feeding whale will exhale underwater, lunge feed to the surface, and be followed shortly by one to three bubble clouds appearing at the surface, closely adjacent to the whale but arriving at the surface after the whale instead of before, as described above.

Behavioral Strategies

It has been our experience that a given humpback whale will generally repeat a fairly rigid feeding pattern over a period of time. However, several individual humpbacks or groups of humpbacks feeding in the same area may or may not display the same feeding strategy. Several examples illustrate this observation.

In two instances on Stellwagen Bank in 1978, all humpback whales (five and seven individuals) within a 20 km^2 area displayed bubble cloud feeding (slow rise type) for an entire 1-h period of observation. Every whale in sight appeared to be using the same strategy.

During two of the three observation periods on one day in 1979, bubble clouds were formed by one individual in the vicinity of extensive schools of American sand lance, while three other whales were lunge feeding (no bubbling associated) several hundred meters away.

On a third occasion, a single humpback on the northern side of a school of American sand lance was observed forming bubble clouds (with apparent subsurface feeding), while three other animals, working the same school of American

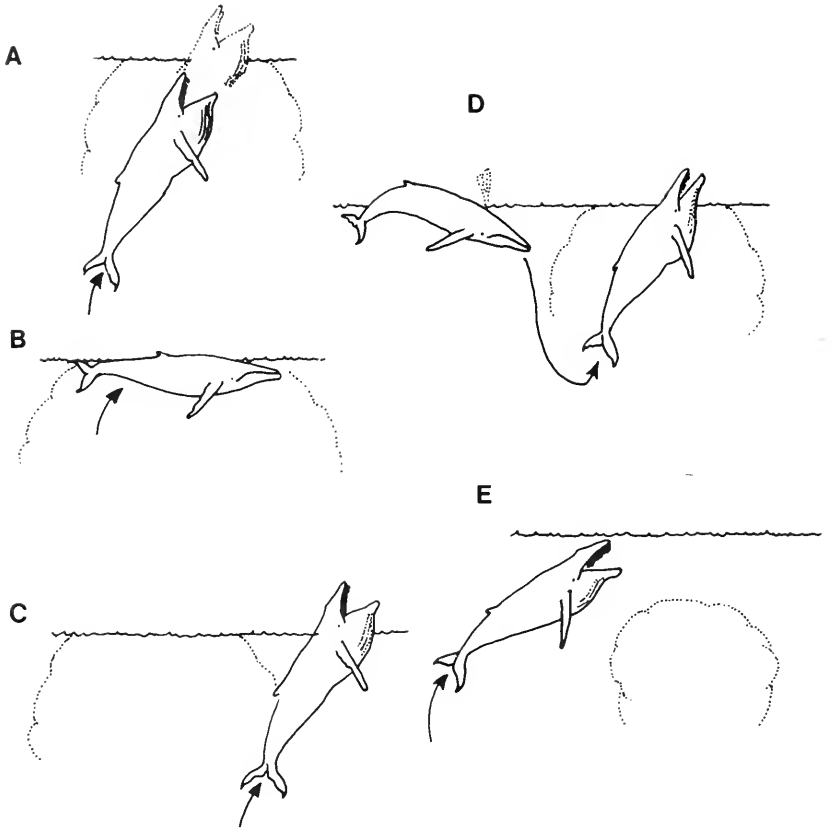

FIGURE 6.—The five feeding variations associated with bubble clouds. A. Whale lunge feeds vertically through the center of the cloud, as in Figure 5. B. Whale apparently feeds underwater and upon completion rises slowly through the center of the spent bubble cloud; the whale's body is on a horizontal plane and the mouth is not agape. C. Whale lunge feeds to one side of cloud. D. Whale surfaces alongside cloud, emits a weak blow, dives, and reappears lunge feeding through the center of the cloud. E. Whale swims vertically up alongside the rising cloud, and then passes horizontally, mouth agape, between the still-rising cloud and the water's surface.

sand lance, were generating bubbles in rows, as well as randomly, and lunge feeding.

Prey Species

Shipboard observations, primarily on Stellwagen Bank, provide direct visual and photographic evidence that concentrated schools of American sand lance are a frequent prey species in the area. American sand lance was identified in 50% of feeding events from the *Dolphin III* on Stellwagen Bank in 1978 and in 75% of observations in 1979. Photographs show American sand lance in the corners of the whale's mouth, being picked up by closely associated birds, and in concentrated surface schools in which the whale is feeding.

At least one other species is a target for humpback feeding. It appeared that humpbacks in the West Quoddy Head area took herring, *Clupea harengus*, close inshore and in coves, using the bubble cloud and lunge feeding techniques on a number of occasions.[5]

DISCUSSION

Humpback whales in the North Atlantic feed on a wide variety of prey species, with krill and schooling fishes the most important (Tomilin 1967). In Canadian waters, humpbacks feed heavily on capelin, with krill second in impor-

[5]S. K. Katona and P. V. Turnbull, College of the Atlantic, Bar Harbor, ME 04609, pers. commun. October 1980.

tance, although the data also suggest haddock, mackerel, whitefish, and sand lance (Mitchell 1973; Sergeant 1975[6]). The American sand lance has been suggested as a prey species in the Cape Cod area by Overholtz and Nicolas (1979). Our direct evidence confirms their observations and demonstrates the importance of this prey species in these waters. The sand lance is similar in size, summer habitat, and schooling behavior to the more northern capelin, *Mallotus villosus* (Overholtz and Nicolas 1979), and therefore may occupy a similar role in the diet of humpbacks in more temperate latitudes. Interestingly, Meyer et al. (1979) reported a significant increase in the relative abundance of sand lance since 1975 on Stellwagen Bank, a trend which was typical of the northwestern Atlantic from Cape Hatteras to the Gulf of Maine.

Indirect evidence suggests herring as a prey species in the northern Gulf of Maine. Watkins and Schevill (1979) also tentatively identified herring, along with pollock, *Pollachius virens*, from Cape Cod waters. These observations will require confirmation as additional knowledge on prey species in New England waters is gained.

With regard to the capture mode of feeding behavior, our observations on lunge feeding closely corroborate those of Watkins and Schevill (1979) and Jurasz and Jurasz (1979). The observations on underwater feeding by humpbacks were almost always in association with bubble structures, although Watkins and Schevill (1979) described several instances of underwater feeding in the absence of such structures.

"Apparent circling behavior" during feeding was reported by Watkins and Schevill (1979). Our description of what we term circular swimming/thrashing behavior expands somewhat on their observations. We speculate that the use of anatomical structures and swimming motion in the manner described bears some generic resemblance to the "flick feeding" reported from Alaskan waters by Jurasz and Jurasz (1979). This would seem to be particularly true for the inside loop behavior we have described. These behaviors may be placed together into a major subdivision of feeding behaviors, the various bubbling behaviors being the other major subdivision.

The effect of the whale's feeding behavior on the prey species, and the advantage conferred to the whale, remains a subject for conjecture, since few data are available. The bubbling behaviors are perhaps the most intriguing. Based on experiments with artificial bubble curtains, it is known that under certain circumstances, curtains of bubbles form an effective barrier to schooling fish (Brett and Alderdice 1958; Smith 1961; Bates and VanDerwalker 1964). Whatever the precise mechanism, it seems reasonable to conclude that humpback whale bubble nets can, and do, effectively corral schools of prey. Whether bubble nets concentrate the prey[7] or merely enclose and maintain naturally occurring concentrations of prey (as hypothesized here) can only be resolved by further study.

The humpback appears well suited to these behaviors; Edel and Winn (1978) have described in some detail the locomotion, maneuverability, and flipper movement required to execute the behaviors described here. It has been suggested (Howell 1970; Brodie 1977) that flashes from the long, white flippers are used to concentrate or herd the prey. This may play a role in the circling behavior, the bubble-netting, and perhaps other types of feeding. In the case of bubble-netting, in addition to their hydrodynamic function, the vertical orientation of the two extended flippers may act in unison with the bubble screen to help form the "curtain" which herds and/or entraps the prey.

While bubbling behavior appears to be commonly associated with feeding (52% of our feeding observations), some caution is in order. Underwater bubbling, even in the presence of feeding activity, may not always be directly related to feeding (see also Watkins and Schevill 1979). Underwater exhalations from humpbacks in nonfeeding situations have also been observed. On occasion, underwater exhalation by humpbacks when approached by ships has been recorded. From field observations and study of photographs, the possibility that some swimming and bubbling behavior may be "play" behavior, particularly when displayed in the presence of closely associated dolphins, is recognized. In the Pacific, Hubbs (1965) described underwater exhalations with no clearly apparent function, and Forestell and Herman[8] described the

[6]Sergeant, D. E. 1975. An additional food supply for humpback (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*). Int. Counc. Explor. Sea, Mar. Mamm. Comm., C.M. 1975/No. 13:1-7.

[7]Earle, S. A. 1979. Quantitative sampling of krill (*Euphausia pacifica*) related to feeding strategies of humpback whales (*Megaptera novaeangliae*) in Glacier Bay, Alaska. Paper presented at The Third Biennial Conference of the Biology of Marine Mammals, 7-11 Oct. 1979, Seattle, Wash.

[8]Forestell, P. H., and L. M. Herman. 1979. Behavior of

apparent use of bubble screens as camouflage by an escort whale in order to protect a calf or mother-calf pair. It is likely that some functions of bubbling still remain to be discovered. At times, bubbling may be purely adventitious.

The humpback possesses a diverse repertoire of feeding behaviors. Whether environmental factors influence the choice of feeding method is presently unknown. Perhaps, as suggested by others (Jurasz and Jurasz 1979; Watkins and Schevill 1979), various prey species or densities elicit different feeding strategies and behaviors. For less mobile prey or high prey densities, relatively simple devices may be sufficient. For more mobile and evasive species, or for more efficient feeding in lower densities, more sophisticated methods may be advantageous.

ACKNOWLEDGMENTS

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THE INTERRELATION OF WATER QUALITY, GILL PARASITES, AND GILL PATHOLOGY OF SOME FISHES FROM SOUTH BISCAYNE BAY, FLORIDA

RENATE H. SKINNER[1]

ABSTRACT

This study investigated monogenetic trematode infestation of the gills and gill pathology of yellowfin mojarra, *Gerres cinereus* (Gerreidae); gray snapper, *Lutjanus griseus* (Lutjanidae); and timucu (needlefish), *Strongylura timucu* (Belonidae) in relation to water quality in south Biscayne Bay, Florida. Two habitats of the three species in the bay, one in the southeast and the other in the southwest, differed in water quality whereas physical and environmental parameters were similar. The water in southwest Biscayne Bay contained high amounts of ammonia, trace metals, and pesticides which were not present in the southeast bay. The gills of hosts from the habitat with inferior water quality were heavily infested with the Monogenea (Platyhelminthes) *Neodiplectanum wenningeri* (on *G. cinereus*), *Ancyrocephalus* sp. (on *L. griseus*), and *Ancyrocephalus parvus* (on *S. timucu*) and suffered from excessive mucus secretion, epithelial hyperplasia, fusion of gill lamellae, clubbing and fusion of filaments, and aneurisms. Only light infestations and little or no abnormal tissue changes were noted in fish from the area of good water quality. The findings led to the conclusion that the pollutants in the water acted as an irritant, stressing the fish, and producing physical and physiological changes which reduced resistance to infestation by Monogenea.

Manmade pollution of coastal waters of southeast Florida has reached a critical level in the most populated areas, causing substantial environmental degradation (Carter 1974) and the loss of valuable fishing grounds, and making some areas unsuitable for recreation. In recent years, the pollution of Biscayne Bay, Fla. (Fig. 1) has become a major issue. The shore of north Biscayne Bay is bordered by Miami and Miami Beach, and lined by bulkheads. It receives a large amount of runoff water from the metropolitan areas (Waite 1976). Although the southwestern part of the bay still retains much of its natural shoreline and mangrove forests, it is broken by drainage canals intended to lower the water level in neighboring agricultural and urban areas. These canals therefore carry agricultural, industrial, and urban wastes into that part of the bay (Waite 1976). The southeastern shoreline of Biscayne Bay is formed by a chain of islands which is part of Biscayne National Park with no major direct sources of water pollution.

The purpose of this study was to investigate if differences existed in the ectoparasite fauna and possible gill pathology in the same three species of fish living in southwest Biscayne Bay in the entrances of three drainage canals on one hand and the relatively clean waters of the southeast bay in the National Park on the other. The effect of water quality on the incidence and intensity of infestation by ectoparasites was investigated along with the frequency and kind of abnormal tissue changes of the gills. Included were those ectoparasites that came close to 100% incidence on their hosts and had a direct life cycle. Three species of Monogenea of the suborder Monopisthocotylea fell into this category.

Monogenea (Platyhelminthes) of the gills are common in fish. Since parasites affect the health of fish, they can be the cause of or a contributing factor to host mortality and epizootics (Iversen et al. 1971). Disease and mass mortality in aquaculture, often occurring under crowded conditions, are known to have been caused by the genera *Gyrodactylus*, *Dactylogyrus*, and *Tetraonchus* (Wobeser et al. 1976). Since exchange of gases in the gills takes place through a single thin epithelial layer separating the blood from the external environment (Anderson and Mitchum 1974), parasites may cause extensive damage to host gill tissue.

Although many adverse circumstances weaken fish and make them more susceptible to diseases, presently available literature is mainly concerned with bacterial diseases (Pippy and

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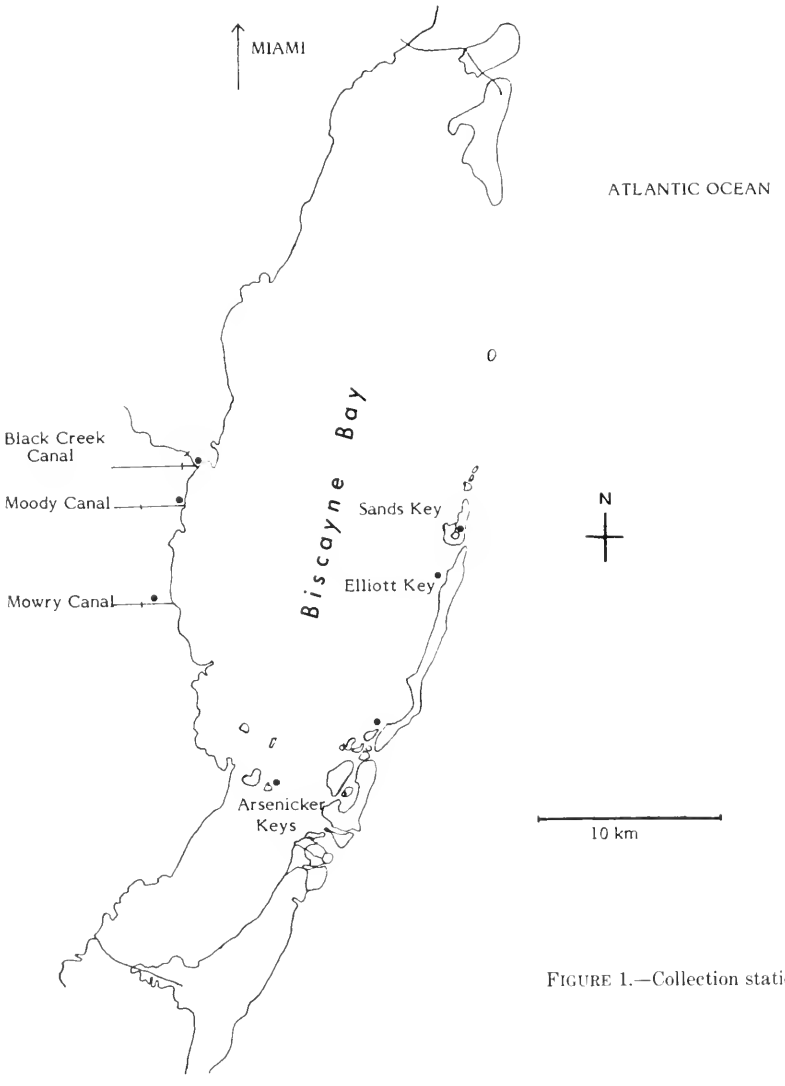

FIGURE 1.—Collection stations in south Biscayne Bay, Fla.

Hare 1969; Bullock et al. 1971; Burrows 1972; Snieszko 1974). Information concerning parasitic diseases in relation to water quality has been obtained in artificial situations such as aquaculture facilities rather than the natural environment. According to Hoffman (1976) eutrophication and pollution probably affect helminth parasites as well as the hosts, but no precise studies have been made. Deleterious effects on various marine biota due to manmade pollution have been investigated, among them disease of fishes and Crustacea (O'Connor 1976; Overstreet and Howse 1977; Sindermann 1979). Overstreet and Howse (1977) suggested that poor environmental conditions may favor parasitic infestation by stressing the host, causing disease and lowering resistance.

In pioneering literature on fish diseases, gill damage other than parasitic was described as due to exposure (Osburn 1911), industrial pollutants (Plehn 1924), and fertilizers (Schäperclaus 1954). More recent literature implicates phenols (Reichenbach-Klinke 1965), ammonia (Reichenbach-Klinke 1966; Smith and Piper 1975), pesticides (Lowe 1964; Walsh and Ribelin 1975), and environmental stress, defined as a change from the normal which reduces the chances for survival (Snieszko 1974). Damage to the gills in response to various toxins in the water was reported by Herbert and Shurben (1964), who suggested

that "sublethal effects of each poison can sum within the individual fish and kill it." Minimal risk, hazard and lethal levels, and median lethal concentrations (LC_{50}, the concentration that kills 50% of the test organisms in 96 h) of certain pollutants in the marine environment are published by the National Academy of Sciences Environmental Studies Board (1972). Although both the National Academy of Sciences and conservation organizations have emphasized the need for ecological information on long-term effects of pesticides on wildlife at sublethal doses, most field studies are done after the animals have been found dead. Mitrovic (1972) asked for studies of subtle damage resulting from long-term exposure at subacute levels. Local studies are needed, since environmental conditions vary with location, and temperature, salinity, and pH play a part in the toxicity of poisons (Trussel 1972). Subtle indications of damage, according to Johnson (1968), may be a change in behavior caused by lowered efficiency of the organism. He suggested that the illustration of physiological and ecological effects of sublethal quantities of environmental pollutants will lead to a more realistic view in establishing tolerance levels for all toxic pollutants. This requires year-round monitoring to take into consideration seasonal variation, variation in drainage as a result of precipitation, runoff, and irrigation, as well as fluctuating physical or chemical factors.

MATERIALS AND METHODS

The study period extended from May 1975 to August 1976. The three host species were yellowfin mojarra, *Gerres cinereus* (Walbaum), a bottom feeder; gray snapper, *Lutjanus griseus* (Linnaeus), a predator; and timucu (needlefish), *Strongylura timucu* (Walbaum), a surface feeder, since they were available on both sides of south Biscayne Bay and remained in one locality for extended periods (Cervigon 1966; Randall 1968; Cressey and Collette 1971; Starck 1971).

Collection stations for the fish were the mouths of Black Creek, Moody, and Mowry Canals; the Arsenicker Keys; Elliott Key; and a canal in Sands Key (Fig. 1). South Florida Water Management District maintains salinity control structures a short distance inland from the southwestern shoreline of Biscayne Bay at Black Creek, Moody, and Mowry Canals. Directly upstream from the gates the water is brackish. The flood gates open automatically according to the difference in the water level on both sides when the water exceeds a certain height on the upland side. For many months during the study period the gates of the salinity structures remained closed because of the low freshwater table inland and the danger of saltwater intrusion into inland wells. Fish were collected downstream from the salinity control structures near the entrances of Moody and Mowry Canals into the bay, at the confluence of Black Creek and Goulds Canals where they enter the bay, in mangrove creeks and close to shore at Arsenicker and Elliott Keys, and in a manmade canal and lagoon in the interior of Sands Key.

Collections were made between April 1975 and August 1976 during three to five trips per week, depending upon weather conditions. The total number of fish collected was 356, of which 186 were from the southwest locations and 170 from southeast Biscayne Bay (Table 1). Only one species was collected on a given day from one area to prevent exchange of parasites from one host species to the other. The yellowfin mojarra were caught by gill net, 75 mm mesh size (stretch), and occasionally on hook and line; the gray snapper on hook and line; and the timucu (needlefish) on hook and line, and by beach seine. Collection trips to the stations were alternated regularly, depending on weather conditions and need. Because of the gear used, size ranges of fish were the same in both localities. Sex ratios were similar, with an average of 52% males and 48% females.

Fish were collected at depths between 0.5 m and 2.5 m. Water samples for the salinity readings were obtained from depths of 0.3 m, 1.0 m, and 3.0 m. An average of 2.5 salinity measurements per month were made at each station and each depth. To avoid contamination a closed, weighted plastic bottle was lowered to the desired depth where it opened and filled with water. Additional salinity data for the years 1975 and 1976 from Black Creek, Mowry, and Moody Canals downstream from salinity structures were made available by the U.S. Geological Survey (USGS) and South Florida Water Manage-

TABLE 1.—Numbers of fish hosts collected in the southeast and southwest locations in Biscayne Bay, Fla., between May 1975 and August 1976.

	S.E. Biscayne Bay	S.W. Biscayne Bay
Gerres cinereus	69	52
Lutjanus griseus	57	80
Strongylura timucu	44	54
Total	170	186

ment District (SFWMD) (unpubl. data). Temperature and dissolved oxygen measurements were taken at 0.3 m and 1.0 m depths. The average of two or three readings represent one measurement. The average number of measurements was two to three per month at each station. Data of hydrogen ion concentration expressed as pH were obtained from the Dade County Department of Environmental Resources Management (DERM) and USGS (unpubl. data).

DERM and USGS obtained routine monthly water quality data for Black Creek, Mowry, and Moody Canals downstream from salinity structures and made them available for this study. The DERM laboratory also made water quality analyses of eight southeast Biscayne Bay water samples collected at intervals of 2 mo. The samples, taken from slick-free water (see Discussion section), were kept in plastic bottles which contained a few milliliters of hydrosulfuric acid for preservation, and were refrigerated until arrival in the laboratory. Chemical analyses were made for total ammonia nitrogen, nitrite, nitrate, phosphate, and total organic carbon. DERM and USGS furnished data on heavy metals in Black Creek and Mowry Canals and pesticides in Black Creek Canal.

Fish were kept alive in an aerated plastic container until arrival and dissection at the laboratory. Body surface, fins, gills, gill covers, and mouth were searched for parasites; the gill arches and single parasites fixed and preserved; and the parasites identified and counted. When parasites were too numerous for total counts, estimations of numbers per gill arch were made from counts per gill filament. Formalin,[2] AFA (alcohol-formol-acetic acid) fixative, and Bouin's solution were used to fix whole gill arches and trematodes. They were preserved in 70% ethanol. For the purpose of identification whole mounts were made of Trematoda using Harris hematoxylin and Permount. Whenever possible, original descriptions of parasites were used for identification together with Yamaguti's (1963, 1971) keys for identification of trematode genera. Histological sections of 12 entire gill arches from 12 fish were examined. Arches were decalcified prior to embedding and cut at 8 μm. Sections were mounted, stained with hematoxylin and eosin (H&E) and Periodic Acid Schiff (PAS). Histological techniques were after the method described by Humason (1972). Statistical evaluation of all station salinity data consisted of calculations of standard deviation (Snedecor and Cochran 1967).

RESULTS

Water Quality

Variations in salinity occur in Biscayne Bay from year to year because of climatic conditions. The salinity readings of all stations were similar during the dry season of 1976, mainly January to June (Table 2). Maximum salinities in both the bay and canal entrances were 40-41‰ at this time. More freshwater discharge into the canals and Biscayne Bay during the rainy season in the fall accounted for a slight drop in salinity and some fluctuation mainly in the canals at that time. The lowest salinity reading from surface water samples from the entrance of Moody Canal in September indicated that freshwater discharge was more noticeable in this narrow canal than in the others. Some salinity measurements were taken immediately after freshwater discharge (see Table 2, footnotes). A typical reading showed that the fresh water flowed as a shallow surface layer about 30 cm deep out of the canals. During freshwater discharge, salinity at the surface varied from 5‰ to 15‰; at a depth of 30 cm it rose by 15-20‰, and at a depth of 1 m it was close to the reading before the discharge, indicating that there was little vertical mixing.

The statistical analysis of monthly averages of salinity data of all stations of 1.0 m depth showed that two-thirds of the values fell within one standard deviation of 1.85 on each side of the mean of 36.8‰. Temperatures reflected seasonal changes at all stations and were similar, with most values between 20° and 30°C (Table 2). Differences may reflect the time of day when readings were taken. Dissolved oxygen concentration fluctuated mainly at canal entrances. Values ranged from 4 ppm to above 8 ppm (Table 2). Values below 6.8 ppm did not occur in southeast Biscayne Bay.

Phosphates, ammonia, nitrites, and nitrates present at the collection sites from May 1975 to August 1976 are listed in Table 3. The southeast Biscayne Bay water quality data were similar to those of de Sylva[3] and Bader and Roessler[4]. In general, southeast bay values were low in all

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

[3]de Sylva, D. P. 1970. Ecology and distribution of postlarval fishes in southern Biscayne Bay, Florida. Univ. Miami

TABLE 2.—Monthly average of salinity, temperature, dissolved oxygen (DO) concentration and pH in southeast Biscayne Bay and southwest Biscayne Bay at Black Creek, Mowry, and Moody Canals, Fla. (at depth 1.0 m).

Location/ date	Salinity (‰)				Temp. (°C)				DO (ppm)	
	No.	Max.	Min.	Avg.	No.	Max.	Min.	Avg.	Avg	pH
S.E. Biscayne Bay										
June 1975	1	34	34	34	2	30	30	30	7.5	—
July 1975	2	35	35	35	3	34	32	32	—	—
Aug. 1975	2	35	35	35	3	34	33	34	6.9	—
Sept. 1975	2	35	35	35	3	34	30	32	—	—
Oct. 1975	4	39	36	37	3	33	29	30	7.8	—
Nov. 1975	3	38	36	37	1	22	22	22	—	—
Dec. 1975	2	38	38	38	1	23	23	23	8.0	—
Jan. 1976	3	38	38	38	3	22	19	20	—	—
Feb. 1976	2	38	36	38	2	20	19	20	8.2	—
Mar. 1976	5	39	38	39	2	25	20	22	—	—
Apr. 1976	2	38	38	38	3	29	25	27	8.1	—
May 1976	3	40	38	39	3	31	24	27	—	—
June 1976	2	40	39	[1]40	3	31	28	29	7.8	—
July 1976	—	—	—	—	3	34	31	32	—	—
Aug. 1976	—	—	—	—	2	33	30	32	—	—
S.W. Biscayne Bay at Black Creek Canal										
May 1975	1	34	34	34	1	29	29	29	4.5	7.4
June 1975	2	37	35	36	1	29	29	29	4.5	7.3
July 1975	4	39	35	38	3	30	30	30	4.7	7.2
Aug. 1975	2	38	38	38	4	31	30	31	4.7	7.3
Sept 1975	4	36	34	35	2	31	31	31	4.2	7.3
Oct. 1975	1	36	36	36	1	29	29	29	5.1	7.5
Nov 1975	3	38	35	37	3	27	27	27	7.2	7.9
Dec. 1975	2	38	36	37	1	22	22	22	5.1	7.5
Jan. 1976	3	38	37	37	3	22	21	22	8.6	7.9
Feb. 1976	1	38	38	38	1	26	26	26	4.3	7.8
Mar. 1976	3	40	38	39	3	25	25	25	5.2	8.0
Apr 1976	2	39	38	39	3	27	25	26	5.3	8.2
May 1976	2	40	39	40	3	28	25	27	3.6	7.4
S.W. Biscayne Bay at Mowry Canal										
June 1975	1	34	34	34	3	30	30	30	4.0	7.8
July 1975	2	35	34	[2]35	3	31	30	31	4.2	7.4
Aug. 1975	4	36	32	[3]35	3	31	31	31	—	7.5
Sept. 1975	2	35	35	35	4	31	30	31	6.2	7.8
Nov. 1975	2	37	36	37	3	30	28	28	7.4	7.8
Dec. 1975	—	—	—	—	2	23	23	23	8.0	8.0
Jan. 1976	1	35	35	35	1	21	21	21	6.5	7.7
Feb. 1976	3	36	35	36	4	22	21	21	7.5	7.9
Mar. 1976	2	40	38	39	3	26	22	25	7.6	8.1
Apr. 1976	2	40	37	39	3	27	25	26	5.2	8.0
May 1976	1	40	40	40	1	26	26	26	5.2	7.4
June 1976	2	38	36	37	2	29	29	29	4.0	7.4
S.W. Biscayne Bay at Moody Canal										
May 1975	—	—	—	—	2	29	29	29	4.0	7.8
June 1975	3	35	34	35	—	—	—	—	—	—
July 1975	—	—	—	—	1	29	29	29	4.2	7.5
Aug. 1975	4	36	36	36	2	31	31	31	4.2	7.5
Sept. 1975	—	—	—	—	1	30	30	30	4.8	7.5
Oct. 1975	1	35	35	35	3	31	29	30	4.5	7.4
Nov. 1975	1	36	36	36	2	29	25	27	6.0	7.8
Dec. 1975	2	38	30	[4]34	3	29	23	26	7.2	7.9
Jan. 1976	1	35	34	35	2	20	20	20	8.0	7.8
Feb. 1976	2	36	35	36	3	22	22	22	8.8	7.8
Mar. 1976	1	37	37	37	1	25	25	25	6.0	7.9
Apr. 1976	—	—	—	—	1	26	26	26	5.2	7.9
May 1976	1	41	41	41	1	26	26	26	4.8	7.8
June 1976	1	36	36	36	1	30	30	30	4.2	7.5

[1]17 July 1976 salinity reading during rainstorm: 10 at surface, 36 at 30 cm depth, 39 at 1 m depth.
[2]30 July 1975 salinity reading, gates open Mowry Canal: 15 at surface, 31 at 30 cm depth, 35 at 1 m depth.
[3]5 August 1975 salinity reading, gates open Mowry Canal: 10 at surface, 27 at 30 cm depth, 32 at 1 m depth.
[4]10 December 1975 salinity reading, gates open Moody Canal: 5 at surface, 20 at 30 cm depth, 30 at 1 m depth.

TABLE 3.—Monthly nutrient[1] values (mg/l) in southeast and southwest Biscayne Bay, Fla., locations (at depth 0.3-1.0 m) (Dade County Department of Environmental Resources Management unpubl. data).

Location/ date	PO_4	TOC	TAN	NO_2	NO_3	Location/ date	PO_4	TOC	TAN	NO_2	NO_3
S.E. Biscayne Bay at Elliot Key						S.W. Biscayne Bay at Mowry Canal					
July 1975	0.00	7.0	0.00	0.00	0.00	May 1975	0.02	—	0.48	0.01	0.00
Sept. 1975	0.00	1.0	0.00	0.00	0.01	June 1975	0.00	6.0	0.44	0.01	0.20
Dec. 1975	0.02	9.0	0.00	0.00	0.07	July 1975	0.00	1.0	0.30	0.02	0.12
Feb. 1976[2]	0.05	12.0	0.00	0.003	0.002	Sept. 1975	0.00	1.0	0.10	0.01	0.02
Apr. 1976	0.00	—	0.00	0.00	0.002	Oct. 1975	0.01	3.0	0.05	0.02	0.68
June 1976	0.017	—	0.00	0.002	0.025	Dec. 1975	0.01	1.0	0.04	0.01	0.50
July 1976[3]	0.338	0.224	0.012	0.00	0.265	Jan. 1976	0.11	3.0	0.04	0.03	0.59
Aug. 1976[3]	0.380	0.336	0.012	0.00	0.168	Feb. 1976[2]	0.40	3.0	0.05	0.01	0.48
						Mar. 1976	0.07	—	—	—	—
S.W. Biscayne Bay at Black Creek Canal						Apr. 1976	0.01	2.0	0.03	0.01	0.17
May 1975	0.32	7.0	0.10	0.01	0.01	May 1976	0.05	3.0	0.04	0.02	0.70
June 1975	0.64	7.0	0.48	0.02	0.30	Aug. 1976[3]	0.01	6.0	0.03	0.01	0.32
July 1975	0.12	4.0	0.72	0.21	0.48						
Aug. 1975	0.48	—	—	—	—	S.W. Biscayne Bay at Moody Canal					
Sept. 1975	0.40	6.0	0.59	0.10	0.56	May 1975	0.00	—	0.06	0.00	0.00
Oct. 1975	0.25	4.0	0.45	0.06	0.43	June 1975	0.02	1.0	0.04	0.00	0.01
Nov. 1975	0.09	—	—	—	—	July 1975	0.00	—	—	—	—
Dec. 1975	0.25	4.0	0.44	0.24	1.5	Sept. 1975	0.01	—	—	—	—
Jan. 1976	0.00	4.0	1.0	0.30	2.1	Oct. 1975	0.02	1.0	0.06	0.02	0.32
Feb. 1976[2]	0.50	6.0	0.51	0.11	1.8	Dec. 1975	0.01	3.0	0.04	0.02	0.48
Mar. 1976	0.18	—	—	—	—	Jan. 1976	0.00	3.0	0.04	0.03	0.50
Apr. 1976	—	6.0	0.03	0.16	1.2	Mar. 1976	0.14	3.0	0.03	0.01	0.30
May 1976	—	1.0	0.32	0.03	0.36						
Aug. 1976[3]	0.04	11.0	0.31	0.01	0.08						

[1]TOC = Total organic carbon, TAN = Total ammonia nitrogen. The term "total" refers to the amount present both in solution and in suspension.
[2]Arsenicker Keys.
[3]Sands Key.

nutrients. Nutrient concentrations were considerably higher in the southwest, especially ammonia values. The water sample taken in April 1976 near Arsenicker Keys contained high total organic carbon compared with the other samples because of the proximity of an extensive mangrove coastline and the presence of mangrove detritus in the water. The two July 1976 water samples from Sands Key were taken in a canal and small lagoon inside the Key surrounded by mangroves and connected to the bay. At low tide, about two-thirds of the bottom muds of the lagoon were exposed, the canal was rich in fish, and wading birds fed in the flats at low tide. The somewhat higher content of ammonia, nitrates, and phosphates was due to decaying vegetation, the exposed mud flats, animal concentrations, and little flushing. Trace metals were present in water samples from the southwest locations only (Table 4). None were detected with standard methods in water samples from the southeast bay. Those pesticides either present or not detected in the water in Black Creek during the time of this study are shown in Table 5. None were detected with standard methods in the southeast bay. As in all the other southeast bay samples, no pesticides or heavy metals were detected in Sands Key samples. The junction of Black Creek and Goulds Canals and the south-

Sch. Mar. Atmos. Sci., Prog. Rep. Fed. Water Qual. Admin., 198 p.

[4]Bader, R. G., and M. A. Roessler. 1971. An ecological study of south Biscayne Bay and Card Sound, Florida. Rosenstiel Sch. Mar. Atmos. Sci., Univ. Miami.

TABLE 4.—Potentially harmful trace metals (μg/l, total) in southwest Biscayne Bay locations of Black Creek and Mowry Canals, Fla., from May 1975 to May 1976 (USGS unpubl. data).

	Black Creek Canal				Mowry Canal				Hazard level to marine biota[1]	Minimal risk level to marine biota[1]	Source
	May 1975	Oct. 1975	Jan. 1976	Apr. 1976	May 1975	Oct. 1975	Jan. 1976	Apr. 1976			
As	2	2	—	2	—	1	1	1	50	10	Paints; pesticides; industry
Pb	4	7	19	20	—	7	9	38	50	10	Gasoline fuel; industry
Mn	4	20	0	0	—	0	0	0	100	20	Industry, paints
Hg	0.2	0.2	0.2	0.5	—	0.1	0.2	0.6	0.1	—	Pesticides; paint plastics and paper industry
Zn	2	2	20	0	—	—	—	—	100	20	Plating industry

[1]Natl. Acad. Sci., Natl. Acad. Eng., Environ. Stud. Board (1972).

TABLE 5.—Pesticides (μg/l) in southwest Biscayne Bay location of Black Creek Canal, Fla., from July 1975 to August 1976 (USGS unpubl. data).[1]

Date	Diazinon[2]	2,4-D[3]	Silvex[4]	Parathion[5]
July 1975	0.02	0.00	0.02	—
Dec. 1975	0.06	0.00	0.00	0.02
Aug. 1976	0.00	0.27	0.10	0.00

[1]Pesticides not found present in Black Creek Canal water samples were: Aldrin, Chlordane, DDD, DDE, DDT, Dieldrin, Endrin, Ethion, Heptachlor, Heptachlorepoxide, Lindane, Malathion, Methyl-parathion, Methyltrithion, PCB, Toxaphene, Trithion, and 2,4,5-T.
[2]0,0-Diethyl 0-(2-isopropyl-6-methyl-4-pyrimidinyl) phosphorothioate.
[3]2,4-Dichlorophenoxy (acetic acid).
[4]2-(2,4,5-Trichlorophenoxy) propionic acid
[5]0,0-Diethyl-0-p-nitrophenyl phosphorothioate.

west bay was found to be the highest in nutrients and trace metals. Direct sources of pollution may have been waste discharge from boats, marinas, agriculture, suburban developments, and the nearby county dump. Slightly lesser amounts were found at the Moody and Mowry stations which were located some distance from inhabited areas. Pesticide data were not available from the Moody and Mowry stations, although chemical pest and weed control conducted at the time along the banks and in the vicinity of the canals would have been a direct source of pesticides in the water.

Parasites

The parasite fauna in both the southeast and southwest Biscayne Bay habitats was similar in kind for all three hosts, consisting mainly of previously reported ectoparasites of marine fishes of the same and related species or those sharing similar habitats. The three monogenetic gill parasites—*Neodiplectanum wenningeri*, *Ancyrocephalus* sp., and *A. parvus*—showed close to 100% incidence and were therefore suitable for this study. Incidence of infestation was as follows: *N. wenningeri* on *G. cinereus*, 97% in southeast Biscayne Bay, 100% in southwest Biscayne Bay locations; *Ancyrocephalus* sp. on *L. griseus*, 100% in southeast Biscayne Bay, 100% in southwest Biscayne Bay; *A. parvus* on *S. timucu*, 100% in southeast Biscayne Bay, 100% in southwest Biscayne Bay.

The difference in intensity of infestation of hosts by these parasites was striking, with few parasites on host gills from the southeast locations and extremely large counts on hosts from the southwest locations (Table 6).

Pathological Changes in Host Gills

Neodiplectanum wenningeri created comparatively little histological disturbance of the gills when infestation was light. Damage was often mechanical and gill lamellae were deflected. In severe cases of infestation, however, the lamellae were covered with *N. wenningeri*, and an increase in mucus production was noticed along with clubbing of filaments where parasites were attached. Similarly, when numerous, *Ancyrocephalus* sp. and *A. parvus* caused pathological changes at the site of attachment. Localized host reaction to the parasites' hooks included epithelial hyperplasia and heavy mucus production (Fig. 2), and the respiratory epithelium was lost in some instances. Often the side of the filament opposite the worm attachment was also affected

TABLE 6.—Averages of some nutrients, trace metals, and pesticides in water samples, and Monogenea and gill pathology of the three host species in southeast Biscayne Bay and southwest Biscayne Bay at Black Creek Canal from May 1975 to August 1976.

	Southeast Biscayne Bay				Southwest Biscayne Bay at Black Creek Canal			
Component	Min.	Avg	Max.	No. of samples	Min.	Avg.	Max.	No. of samples
Total ammonia nitrogen mg/l	0.00	0.00	0.012	6	0.03	0.45	1.0	11
Arsenic μg/l	0.00	0.00	0.00	6	2.0	2.0	2.0	3
Lead μg/l	0.00	0.00	0.00	6	4.0	12.5	20.0	4
Manganese μg/l	0.00	0.00	0.00	6	4.0	6.0	20.0	4
Mercury μg/l	0.00	0.00	0.00	6	0.2	0.28	0.5	4
Diazinon μg/l	0.00	0.00	0.00	6	0.02	0.026	0.06	3
2,4-D μg/l	0.00	0.00	0.00	6	0.00	0.09	0.27	3
Silvex μg/l	0.00	0.00	0.00	6	0.00	0.04	0.10	3
Parathion μg/l	0.00	0.00	0.00	6	0.00	0.01	0.02	2
Neodiplectanum wenningeri no./gill arch	0.00	0.625	5	69	25	72.5	>100	52
Ancyrocephalus sp. no./gill arch	0.1	1.4	8	57	69	124.75	>500	80
Ancyrocephalus parvus no./gill arch	0.3	2.25	4.5	44	61	89.25	>200	54
Pathological changes[1]	None	None	Slight	170	Moderate	Severe	Severe	186

[1]Slight = mucus production above normal; moderate = heavy mucus production and epithelial hyperplasia; severe = fusion of lamellae, loss of structure.

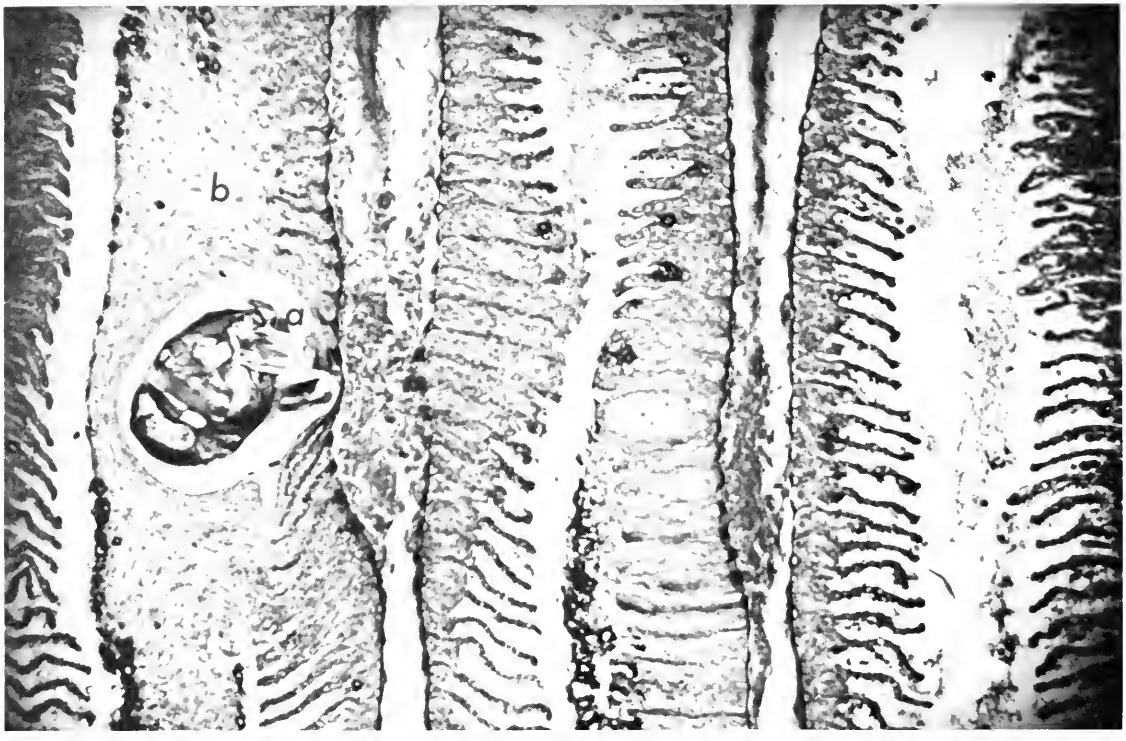

FIGURE 2.—Photomicrograph of *Ancyrocephalus* sp. on the gills of *Lutjanus griseus*, 22.0 cm SL, from southwest Biscayne Bay, Fla. (PAS, 75×) showing hyperplasia, loss of respiratory epithelium, excessive mucus, lamellar fusion, and aneurisms. a) parasite; b) mucus.

in a similar manner (Fig. 3). In addition to injury caused by the hooks of the parasite, the lamellae were deflected and adhered to each other, thus reducing the gill surface effective for gas exchange. In severe cases when a number of worms were attached to the tips of filaments, clubbing of filaments was almost always present, as was obliteration of normal filament structure. The affected filaments appeared white in fresh preparations and the gills were congested with mucus.

Histological changes of the gills not associated with parasites were found in hosts from southwest Biscayne Bay stations. Few southeast Biscayne Bay fish showed above-normal production of mucus in the gills. Increased mucus production was evident in all fish from the southwest locations, and pathological changes ranged from moderate to severe (Table 6). Abnormal color changes were frequent in southwest Biscayne Bay fish and were usually associated with overproduction of mucus which congested the gills. Histological sections of gills from these fish showed that whole filaments were lined with mucus and that it filled the spaces between the filaments. Additionally, mucus-producing cells were concentrated, sometimes in several layers, at the tips of gill filaments which had lost their normal structure. Fusion of gill lamellae along entire filaments, epithelial hyperplasia, clubbing of lamellae or obliteration of lamellar structure, aneurisms, and clubbing of filaments occurred frequently, along with proliferation of cells at the bases of lamellae.

DISCUSSION

According to Grundmann et al. (1976), helminth populations in a natural environment are well regulated to a point of host comfort. Although the results from the southeastern habitat in this study agreed with this statement, those from the southwest bay locations did not. Disease caused by parasites often requires exogenous as well as endogenous factors (Sindermann 1979). Exogenous factors, as defined by Cameron

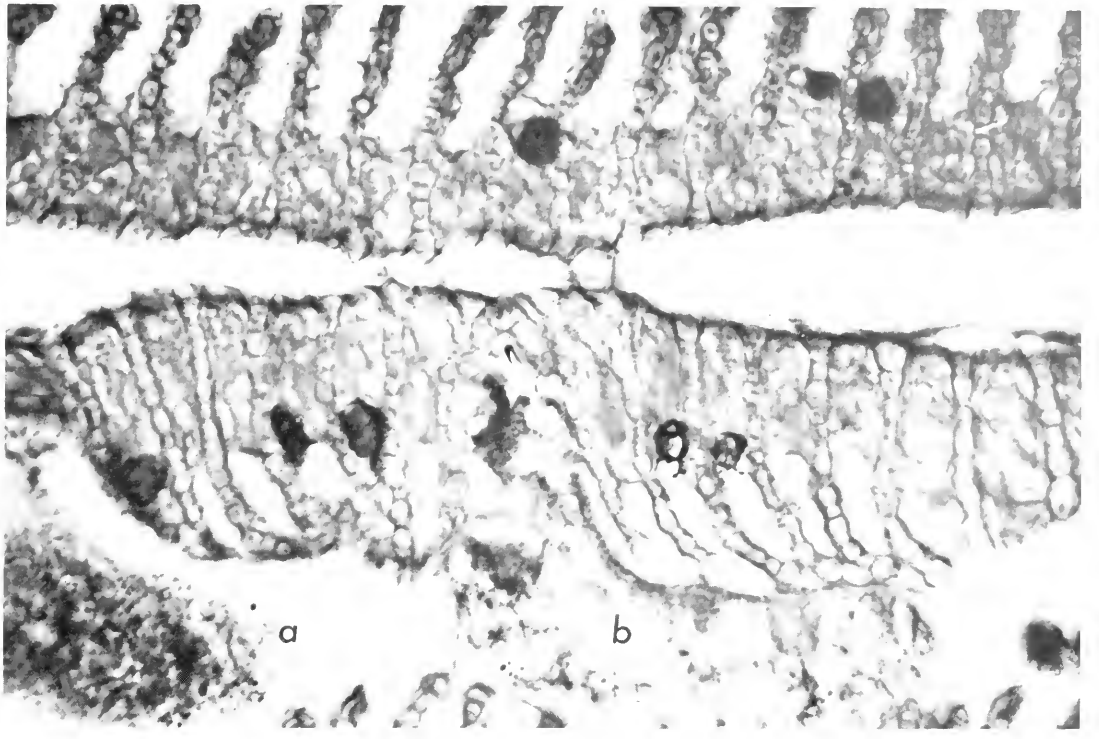

FIGURE 3.—Photomicrograph of two *Ancyrocephalus parvus* on the gills of *S. timucu*, 24.3 cm SL, from southwest Biscayne Bay, Fla. (PAS, 300×). Lamellae are deflected and obstructed. a) and b) parasites.

(1958), are alterations in the ecology of the parasites or hosts by some abnormal or unnatural event, most often manmade.

The most outstanding difference between the southeast Biscayne Bay and southwest locations was the difference in chemical water quality. According to Klontz (1972), fish are so intimately associated with their aqueous environment that physical or chemical changes in this environment are often rapidly reflected as measurable physiological changes in the fish. In general, reactions of fish gills to an irritant include inflammation, hyperplasia, lamellar fusion, excessive mucus production, clubbing of filaments or lamellae, and formation of aneurisms.

Aneurisms may be a specific tissue reaction due to injury or toxic substances, especially ammonia or herbicides in the water or food (Eller 1975). Ammonia frequently has been reported to cause extensive gill damage. Although much of the data on the degree of toxicity of ammonia is not satisfactory (National Academy of Sciences Environmental Studies Board 1972), it has been shown that the more toxic component of ammonia solutions is the unionized ammonia (NH_3). An increase in pH from the normal level increases the toxicity, because along with temperature it controls the degree of dissociation (Trussel 1972). A decrease in dissolved oxygen concentration increases the toxicity of unionized ammonia (National Academy of Sciences Environmental Studies Board 1972). Even low concentrations may cause pathological changes in marine and freshwater organisms (Doudoroff and Katz 1950; Flis 1968; Larmoyeux and Piper 1973). In addition to exhibiting gill damage, after exposure to NH_3 freshwater fish were susceptible to ectoparasites, according to Reichenbach-Klinke (1966). Prolonged exposure to nonlethal dosage of ammonia in salmon led to hyperplasia of gill epithelium and epizootic bacterial gill disease in a study by Burrows (1964).

Pollutants such as metals and pesticides show similar effects on fish gills (Gardner 1975). The LC_{50} and sublethal effects of pesticides are presently under scrutiny. According to Anderson (1971), for pollutants not to influence the physiology and behavior of fish, "safe" concentrations

should be 0.01-0.05 of the lethal concentrations. Since a small rise in temperature or salinity can shift the LC_{50} by one order of magnitude (Eisler 1972), most pesticides may be more harmful than previously assumed. A synergistic effect of several sublethal concentrations of pollutants is possible. They may exist in such low concentrations that conventional analysis or collection methods will not detect them, especially herbicidal contaminants. However, Seba and Corcoran (1969) found that surface slicks formed by a film of organic matter concentrated pesticides in southwest Biscayne Bay to detectable levels, up to 137 times as much as slicks in the Florida Current.

Although the reaction of gill tissue to toxic chemicals appears to be nonspecific in regard to the particular chemicals present, and it is therefore difficult to indict any one particular component or group of components in nature, the overall result of gill damage is impairment of function. Regardless of cause, pathological changes reduce the useful respiratory surface and make gas exchange difficult, which stresses the fish and eventually weakens it.

Disease has been known to change behavior in fish (National Academy of Sciences 1973) and influence their chance for survival. Impaired function of an organ and reduced efficiency require expenditure of energy which cannot be used for other life processes such as feeding, reproduction, and predator avoidance. In case of gill damage, metabolic activity must be reduced to a minimum in order to reduce oxygen demand (Wedemeyer et al. 1976), and the fish become weakened and stressed. Selye's (1950) definition of stress was used in reference to fish by Wedemeyer (1970): "the sum of all the physiological responses by which an animal tries to maintain or reestablish a normal metabolism in the face of a physical or chemical force." Unfortunately, some of the metabolic changes may also contribute to increased susceptibility to disease (Wedemeyer et al. 1976).

When fish are weakened by environmental factors, chemicals, or poor nutrition, their resistance to infestation and infection by Monogenea, *Trichodina*, and bacteria is reduced (Schäperclaus 1954; Wedemeyer et al. 1976). These facts are well known to the aquaculture and aquarium industries. Most research on immune reactions is done in human and veterinary medicine, but parallels can be drawn since fishes' immune systems, although less advanced, resemble those of other vertebrates (Sindermann 1970). Mucus antibody may be active against some external infestations (Anderson 1974); thus, a parasite must be able to avoid the immune reaction of the host (Williams 1970). Stress-provoked physiological changes may cause a disturbance of the host's immune system, and damaged or irritated gills can then become heavily infested with parasites. Snieszko (1974) shared the belief of other scientists that the aggravating effect of stress from various types of pollution caused a high incidence of infectious disease in fishes, and mentioned that this belief, unfortunately, was not yet adequately documented. Sindermann (1979) summarized some of the recent supporting evidence that toxins have a deleterious effect on the immune response of fishes. This study of Biscayne Bay fishes suggests that, in the presence of sublethal quantities of pollutants in a natural marine environment, fish suffered from gill damage which produced stress, physiological and physical compensation, leading to weakening, reduced immunity, and heavy parasitic infestation.

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THE EFFECT OF PROTEASE INHIBITORS ON PROTEOLYSIS IN PARASITIZED PACIFIC WHITING, *MERLUCCIUS PRODUCTUS*, MUSCLE

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ABSTRACT

Since the enactment of the Fishery Conservation and Management Act of 1976, the U.S. fishing industry has intensified its interest in Pacific whiting, *Merluccius productus*, as an additional food resource. In some fishing areas, Pacific whiting is infected with a protozoan parasite, *Myxosporidia kudoa*, which produces a proteolytic enzyme that degrades the textural quality of muscle as it is processed or cooked.

Several enzyme inhibitors were evaluated for their potential to inactivate the enzyme, thereby preserving the texture of the fish during processing. It was found that protease inhibitors such as those found in egg white, potato, and soy and lima beans were ineffective as inhibitors. Compounds that react with sulfhydryl groups, on the other hand, were found to be active inhibitors. These compounds include hydrogen peroxide (free and alkaline), potassium bromate, iodoacetate, and N-ethylmaleimide. The most promising results were obtained with potassium bromate or combinations of dibasic phosphate peroxide and potassium bromate. These reagents mixed into ground parasitized pacific whiting muscle inhibited proteolysis sufficiently during frozen storage and later cooking to maintain texture comparable with nonparasitized fish.

The Fishery Conservation and Management Act of 1976 has intensified the interest of the fishing industry in Pacific whiting, *Merluccius productus*, as an additional food resource. Although Pacific whiting has been extensively fished by the Russian and Polish fishing fleets, it has attracted only slight commercial interest in the United States, primarily because its texture and color are somewhat less desirable than that of other gadoid species such as cod and haddock. In 1970, Dassow et al. observed that the textural change in cooked Pacific whiting was due to the presence of a protozoan parasite, *Myxosporidia kudoa*. This parasite produces a proteolytic enzyme capable of breaking the chemical bonds of the muscle fibers which are responsible for the characteristic texture of fresh fish. The activity of the enzyme increases as the temperature increases. Thus, during conventional processes such as baking, broiling, or pan frying, the gradual increase in heat enhances proteolysis until the product reaches the temperature of inactivation of the enzyme. One method of handling the problem of the parasitic enzyme is rapid cooking (deep-fat frying of sticks and portions) where the temperature of inactivation is achieved before proteolysis destroys the texture of the fish (Patashnik et al.[2]). Another possibility would be to inactivate the enzyme with an inhibitor.

In the work presented here, several enzymic inhibitors were evaluated to determine their effectiveness in inhibiting proteolysis in Pacific whiting muscle. The concentration of enzyme inhibitor sufficient to prevent organoleptic textural alteration was also determined.

METHODS

Pacific whiting were caught off the coast of Astoria, Oreg., by commercial trawlers, filleted and frozen within 24 h, and stored at −20°C.

The presence of the parasite was determined directly by visual evidence of black and white spores, by microscopic identification of the spores, or, indirectly, by baking a segment of muscle in a covered container for 20 min at 162°C. Soft or mushy muscle indicated the presence of the parasitic enzyme.

To ascertain the effects of enzyme inhibitors under uniform conditions, tests for proteolytic activity were carried out on diluted blends of fish

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[2]Patashnik, M., H.S. Groninger, H. Barnett, G. Kudo, and B. Koury. 1981. Pacific coast whiting (*Merluccius productus*). I. Abnormal muscle texture caused by myxosporidian-induced proteolysis. In prep., 34 p. Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA, 2725 Montlake Blvd. E., Seattle, WA 98112.

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muscle and on ground (minced) muscle. Conditions for testing were kept close to those under which we knew the parasitic enzyme functioned. The pH was maintained at that of the fish (6.8), the substrate was the fish muscle, and the temperature was moderate (45°C).

Blended Fish

Blended fish muscle was prepared by blending two parts 0.1 M NaCl with one part ground fish in a Lourdes Blender[3] in a quantity large enough to serve for several tests. The pH (6.8) of the solutions of the various potential inhibitors was maintained by the addition of dilute NaOH or HCl. In a 50 ml polycarbonate tube, 2 ml of the blended fish was mixed with 1 ml 0.1 M NaCl, as a control, or with 1 ml of the potential inhibitor. The tubes, covered with parafilm, were incubated for 90 min at 45°C. Duplicate samples of the control and test material were kept at 0°C in order to know the soluble protein level before incubation. This figure was subtracted from the quantity of soluble protein that was the result of increased proteolysis in the incubated sample. The reaction was stopped by the addition of 3 ml of 10% trichloroacetic acid. After 30 min at room temperature, the tubes were centrifuged at 9,750 g for 10 min. Protein determinations by the Lowry method (Lowry et al. 1951) were done on 1 ml of the supernatant. The effectiveness of the inhibitor was gauged by comparison of the proteolysis of the control (0.1 M NaCl) with that of the potential inhibitor. Since over a period of time the amount of proteolysis was bound to vary, a control was run with each experiment. In order to calculate the amount of inhibition, an arbitrary figure of 100% was assigned to the control and the effectiveness of the inhibitor was expressed as percent inhibition by the following formula:

$$\frac{\text{g protein/ml of test}}{\text{g protein/ml of control}} \times 100 = \% \text{ proteolysis}$$

$$100 - \% \text{ proteolysis} = \% \text{ inhibition.}$$

Ground Fish

Ground fish was prepared by putting partially frozen fillets through a 4mm die. Ten parts of ground fish were thoroughly mixed with 1 part of 0.1 M NaCl or the inhibitor solution. Three grams of this material was incubated in a 50 ml covered polycarbonate tube for 30 min at 45°C. The reaction was stopped by the addition of 3 ml of 10% trichloroacetic acid. The remaining treatment was the same as with the blended fish.

Preparation of Ground Fish Blocks for Storage

A quantity (about 200 g) of the ground parasitized Pacific whiting was mixed with 0.1 M NaCl (approximately the ionic strength of muscle) as a control or an inhibitor in the ratio of 10 parts fish to 1 part solution. Before the blocks were placed in storage, aliquots were taken to test for inhibition and inhibitor residues. The blocks (3″ × 1″ × 8″) were stored at −20°C for 1 mo. At the end of the month, aliquots were retested for inhibition and inhibitor residues.

Effect of Proteolytic Inhibition on Texture

The blocks of parasitized whiting made for the storage study and a similar block made from nonparasitized Pacific whiting were used to test the effectiveness of maintaining texture by inhibiting proteolysis. Duplicate portions (3″ × 1″ × ½″) were cut from each block and baked in a covered dish (3½″ × 2″ × 1½″). The baked portions were randomly mixed before presenting them to an experienced panel for texture and organoleptic evaluation. In order to express the results in numerical values, numbers were assigned to the texture categories: firm (1); soft (2); mushy (3). Aliquots were taken at the same time to test for percent inhibition.

Oxidative Effect on Amino Acids

Amino acid analyses, using the Beckman 118 CL Amino Acid Analyzer (Spackman et al. 1958), were done on acid hydrolysates of nonparasitized fish, parasitized fish with no treatment, and parasitized fish which had been treated with either 0.5% disodium phosphate peroxide plus 0.025% potassium bromate or 0.5% dipotassium phosphate peroxide plus 0.025% potassium bromate.

Enzyme Inhibitors

All chemicals were of reagent grade. Trypsin

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

inhibitors were purchased from Sigma Company. Dibasic phosphate peroxides were prepared in our laboratory according to the method of Nakatani and Katagiri (1970). The potato extract was prepared in our laboratory according to the method of Melville and Ryan (1972).

Test for the Presence of Peroxides or Bromates

The following method of measuring peroxides and bromates was adapted from two methods, that of Price and Lee (1970) and that of the Association of Official Analytical Chemists handbook (1975):

4 ml H_2O
1 ml of oxidant standard or 1 g fish
1 ml saturated KI
1 ml 0.001 M ammonium molybdate in 1 N H_2SO_4.

Shake for 1 min, titrate to a light yellow with 0.1 N sodium thiosulfate, and add a few drops of 1% starch; continue titrating to the end point. Both hydrogen peroxide and potassium bromate liberate iodine by oxidation; therefore, this method can be used to indicate the presence of either one. Quantification was determined by comparison with a known standard expressed in milliequivalents.

RESULTS AND DISCUSSION

Tests with Blended Fish

Blended fish was used to test a variety of potential inhibitors which are listed with concentrations and results in Table 1. The enzyme inhibitors tested included trypsin inhibitors from four sources: soybeans, lima beans, turkey egg white, and chicken egg white. We also tested crude potato extract which has been shown to contain several protease inhibitors (Melville and Ryan 1972; Ryan et al. 1974; Bryant et al. 1976; Hass et al. 1976). None of the tested enzyme inhibitors caused significant inhibition in concentrations that would be suitable for use in food systems.

From the remaining potential inhibitors which included metal chelators, oxidizers, and sulfhydryl binding compounds, we found hydrogen peroxide, potassium bromate, dibasic phosphate peroxides, iodoacetate, and N-ethylmaleimide to warrant further investigation. The reaction with iodoacetate and N-ethylmaleimide indicated that we were dealing with a thiol enzyme.

TABLE 1.—Protease inhibitors.

Inhibitor	Concentration	Active site	Effect[1]
EDTA	0.3×10^{-1} M	Chelates, Metals	+
	$0.3\cdot10^{-3}$ M		+
	0.3×10^{-5} M		+
Sodium pyrophosphate	$0.3\cdot10^{-1}$ M	Mg, Mn, Zn, other	
	0.3×10^{-3} M	metals	±
	$0.3\cdot10^{-5}$ M		±
Sodium oxalate	$0.3\cdot10^{-1}$ M	Ca, Mg	±
	0.3×10^{-3} M		
Cysteine	$0.3\cdot10^{-1}$ M	Fe, Cu, other metals	+
	$0.3\cdot10^{-3}$ M		±
	0.3×10^{-5} M		±
o-Phenanthroline	0.3×10^{-2} M	Fe, Co, Zn, other	−
	$0.3\cdot10^{-4}$ M	metals	±
Sodium fluoride	$0.3\cdot10^{-1}$ M	Mg, Ca, other metals	
	0.3×10^{-3} M		±
Iodoacetate	0.3×10^{-1} M	Sulfhydryls, imid-	−
	0.3×10^{-2} M	azoles, thio ethers	−
	2.0×10^{-2} M		−
N-ethylmaleimide	0.3×10^{-2} M	Sulfhydryls	−
	1.5×10^{-2} M		−
	0.75×10^{-2} M		−
Hydrogen peroxide	1.0%	Oxidizes	−
	0.1%		−
	0.5%		−
Disodium phosphate peroxide	0.3%	Oxidizes	−
	0.5%		−
Dipotassium phosphate peroxide	0.3%	Oxidizes	−
	0.5%		−
Potassium bromate	0.05%	Oxidizes	−
	0.025%		−
	0.001%		−
Soybean	1 mg/ml	Trypsin	±
Lima bean	5 mg/ml	Trypsin	±
Chicken egg white	5 mg/ml	Trypsin	±
Turkey egg white	5 mg/ml	Trypsin	±
Potato extract	2.5 mg/ml	Chymotrypsin	±
	5.0 mg/ml	Carboxypeptidase	±
	10.0 mg/ml	Serine endopeptidase	±
		Metallocarboxypeptidase	±

[1]Increased proteolysis +, decreased proteolysis −, no signficant change ±.

Tests with Ground Fish

Both hydrogen peroxide (H_2O_2) and potassium bromate ($KBrO_3$) are currently being used in the U.S. food industry to impart desired functional and organoleptic properties to the foods to which they are added. For example, $KBrO_3$ is used in breadmaking to improve the physical properties of the dough (Tsen 1968). H_2O_2 has been used as a preservative in dairy products (Cuq et al. 1973) and as a bleaching agent in some fish products (Sims et al. 1975; James and McCrudden 1976). The dibasic phosphate peroxides have been used as a stablilizer for H_2O_2 in various food products such as soy products, meat, fish, and cereals (Pintauro 1974).

After testing for inhibition effects in the (model) blended system, tests were conducted on ground (minced) parasitized Pacific whiting to test those which demonstrated inhibitory potential and could be used in food systems.

Hydrogen Peroxide

In the ground parasitized Pacific whiting, hydrogen peroxide was significantly less effective in inactivating the proteolytic enzyme than it had been with the blended fish. This was explained by the fact that catalase is known to be present in muscle to destroy hydrogen peroxide formed in aerobic muscle fiber (Deisseroth and Dounce 1970). There was a difference between the blended and ground muscle both in protein concentration and distribution of the catalase. In order to demonstrate the difference more specifically, we compared the protein concentration and the catalase activity in the two systems. Proteins were determined by the macro-Kjeldahl, percent protein N method. Catalase activity was determined by measuring the disappearance of peroxide residues after 0.3% H_2O_2 (0.146 meq) was mixed with 1 g of blended or ground fish. The results in Table 2 show 40% less protein, which includes catalase, in blended fish than in ground fish. When 0.3% H_1O_2 was added to the blended fish, hydrogen peroxide was more slowly degraded and thereby had longer contact time with the enzyme of the parasite. The location of the catalase was shown by washing out all intercellular catalase from ground muscle, then reinstituting the catalase activity by crushing or manipulating the washed muscle fibers. A concentration of 3% H_2O_2 was needed to counteract all catalase activity, but a concentration of this magnitude also destroyed the tissue structure. It was obvious that hydrogen peroxide alone would be impractical to use as a protease inhibitor.

Potassium Bromate

Because of the difference in protein concentration in ground fish, it was necessary to increase the concentration of potassium bromate from 0.01% to 0.05% in order to achieve a 63-66% inhibition of proteolytic activity. This was shown to be sufficient to maintain the texture of parasitized Pacific whiting.

Tsen (1968) suggested that there was a synergistic effect between potassium bromate, a slow oxidizer, and faster oxidizers such as iodates, acetone peroxide, or azodecarbonamide; therefore, potassium bromate was tested with hydrogen peroxide in varying concentrations. The results were not synergistic but 0.025% $KBrO_3$ with 0.5% H_2O_2 was as effective as 0.05% $KBrO_3$ (Table 3).

TABLE 2.—Comparison of protein concentration and peroxide residues in blended or ground parasitized Pacific whiting.

Treatment of fish	Percent protein N	% peroxide residues remaining	
		0 time	5 min
Blended fish	9.88	100 (0.146 meq)	28 (0.041 meq)
Ground fish	16.51	76 (0.110 meq)	9 (0.010 meq)

TABLE 3.—Effect of hydrogen peroxide and potassium bromate on proteolysis in ground parasitized Pacific whiting.

Oxidant	% inhibiton
Control—no treatment	0
0.5% H_2O_2	43
0.05% $KBrO_3$	63
0.025% $KBrO_3$	47
0.01% $KBrO_3$	35
0.05% $KBrO_3$ in 0.5% H_2O_2	66
0.025% $KBrO_3$ in 0.5% H_2O_2	64

Dibasic Phosphate Peroxides

The adduct of hydrogen peroxide with dibasic phosphates has been found to facilitate the use of hydrogen peroxide by stabilizing it in food systems (Pintauro 1974). It seemed possible that these compounds might protect hydrogen peroxide from catalase long enough for it to be effective in inhibiting proteolysis. We tested 0.3% and 0.5% of both disodium phosphate peroxide ($Na_2HPO_4 \cdot H_2O_2$) and dipotassium phosphate peroxide ($K_2HPO_4 \cdot H_2O_2$) with ground parasitized Pacific whiting. When these compounds were compared in terms of milliequivalents of peroxides with equivalent concentrations of hydrogen peroxide alone, disodium phosphate peroxide had 23% milliequivalents of peroxide and dipotassium phosphate peroxides 15%. The dipotassium phosphate peroxide seemed less stable than disodium phosphate peroxide judging from its effervescence. Both dibasic phosphate peroxides were tested alone and with potassium bromate (Table 4). As found earlier in combination with hydrogen peroxide, 0.025% $KBrO_3$ enhanced the proteolytic inhibition of both concentrations of dibasic phosphate peroxides which meant effective inhibition could be achieved with lower concentrations of each of the oxidants.

The results of testing these inhibitors established concentrations and combinations which

TABLE 4.—Effect of dibasic phosphate peroxide on proteolysis in ground parasitized Pacific whiting.

Oxidant	% inhibition
Control—no treatment	0
0.3% $Na_2HPO_4 \cdot H_2O_2$	35
0.3% $K_2HPO_4 \cdot H_2O_2$	9
0.3% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	64
0.3% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	62
0.5% $Na_2HPO_4 \cdot H_2O_2$	45
0.5% $K_2HPO_4 \cdot H_2O_2$	24
0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	73
0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	67

were effective in inactivating the parasitic enzyme in parasitized Pacific whiting. We then determined whether 1) the inactivation would be maintained during a freeze-thaw cycle after 1 mo of storage at −20°C, 2) inactivation was sufficient to maintain a desirable texture, and 3) the treatment with oxidizing agents would adversely affect the amino acids, thereby decreasing the nutritional quality of the protein.

Effect of Frozen Storage

The prolonged effect of frozen storage on inhibition was determined on samples of ground parasitized Pacific whiting treated with various inhibitors. Aliquots of these samples were tested at the time of preparation for percent inhibition and the presence of oxidant residues. All samples were stored at −20°C for 1 mo at which time these tests were repeated, and as the results show in Table 5 there was no decrease in the inhibition of proteolysis. The ground fish treated with 0.5% H_2O_2 had no detectable residues even immediately after treatment, but maintained the inactivity of the enzyme. The residual bromate was dependent on concentration. The samples containing 0.025% and 0.05% $KBrO_3$ still had slight amounts of bromate. Bushuk and Hlynka (1960) reported that 80 ppm of bromate in bread dough disappeared completely after baking for 20 min. We baked portions of ground fish, treated with 0.05% $KBrO_3$, for 20 min at 162°C. There were no detectable residues indicating there would not be significant residues in normally cooked fish.

Effect of Inhibition on Texture

Results of the organoleptic evaluation for texture are shown in Table 6. These results demonstrate that there is a correlation between the percentage of inhibition and the maintenance of firm texture. Samples which had the highest inhibition were judged to have texture comparable with nonparasitized fish.

Oxidative Effect on Amino Acids

Some amino acids are susceptible to oxidation, particularly methionine which is readily oxidized to methionine sulfoxide and, under severe conditions, to methionine sulfone. We were using relatively mild conditions compared with other investigators, but we lacked information on the effect of potassium bromate or the combination of potassium bromate and hydrogen peroxide. We therefore compared the amino acid profiles of acid hydrolysates of nonparasitized Pacific whiting, parasitized with no treatment, and two samples of parasitized ground fish, one of which was treated with 0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$, the other with 0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$. We compared the profiles for differences that might suggest significant destruction of any of the amino acids. Acid hydrolysis converts methionine sulfoxide to methionine so a difference would only show if methionine were converted to methionine sulfone. No significant differences were found in any of the amino acids (Table 7).

TABLE 5.—Storage study of oxidants in ground parasitized Pacific whiting.

Oxidant	% inhibition		Oxidant residue	
	0 time	1 mo	0 time	1 mo
Control—no treatment	0	0	0	0
0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	73	81	+[2]	+
0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	67	75	+	+
0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.01% $KBrO_3$	62	59	+	N.D.[3]
0.5% $K_2HPO_4 \cdot H_2O$ + 0.01% $KBrO_3$	37	46	+	N.D.
0.5% H_2O_2	49	52	N.D.	N.D.
0.05% $KBrO_3$	66	66	+	+
0.5% H_2O_2 + 0.025% $KBrO_3$	63	69	+	+
0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.5% H_2O_2	34	47	+	N.D.

[1]Storage at −20°C.
[2]+ = presence of residue oxidant.
[3]N.D. = not detectable.

TABLE 6.—Texture evaluation of treated parasitized Pacific whiting.

Sample and treatment	Texture evaluation	% inhibition
Nonparasitized Pacific whiting	[1]1.1	
Parasitized Pacific whiting—no treatment	2.6	
Parasitized Pacific whiting treated with 0.5% H_2O_2	2.6	13
Parasitized Pacific whiting treated with 0.05% $KBrO_3$	1.1	69
Parasitized Pacific whiting treated with 0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	1.4	63
Parasitized Pacific whiting treated with 0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$	1.8	64
Parasitized Pacific whiting treated with 0.5% $K_2HPO_4 \cdot H_2O_2$	2.8	28

[1]Categories: 1 = firm, 2 = soft, 3 = mushy.

Treatment of Fillets

Since a large portion of any food fish such as Pacific whiting is sold in the form of fillets, it would be preferable to treat the fillets as well as the minced fish. Recently Spinelli[4] reported on the use of adding aqueous additives into fillets by high pressure injection. The work showed that it is possible to disperse precisely given amounts of aqueous additives into fillets taken from several species of fish.

SUMMARY

The proteolytic activity in minced parasitized Pacific whiting can be effectively inhibited by the addition of hydrogen peroxide, potassium bromate, dibasic phosphate peroxides, iodoacetate, and N-ethylmaleimide. In human food systems, the only acceptable compounds of those mentioned to achieve this inhibition are hydrogen peroxide, potassium bromate, or the dibasic phosphate peroxides. The most effective inhibitors at low concentrations were 0.05% $KBrO_3$ and either 0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$ or 0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$. These inhibitors retained their inhibitory effect during 1 mo of storage at −20°C. The inhibition was sufficient to maintain a firm texture when portions of the treated ground parasitized Pacific whiting were cooked. Catalase in whiting muscle rapidly degraded added hydrogen peroxide, but did not destroy potassium bromate; however, potassium bromate was reduced to undetectable levels when the material was cooked.

TABLE 7.—Percent of amino acid in hydrolysate of ground Pacific whiting muscle.

Amino acid	Non-parasitized	Nontreated parasitized	0.5% $Na_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$ treated	0.5% $K_2HPO_4 \cdot H_2O_2$ + 0.025% $KBrO_3$ treated
Aspartic acid	9.4	9.5	9.6	9.6
Threonine	4.5	4.9	4.6	4.6
Serine	4.8	5.0	5.0	5.0
Glutamic acid	13.6	13.6	13.8	13.8
Proline	3.3	3.4	3.4	3.6
Glycine	7.2	7.0	7.0	7.0
Alanine	8.8	8.4	8.7	8.5
Valine	5.6	5.5	5.6	5.5
Methionine	2.6	2.7	2.6	2.7
Isoleucine	4.2	4.2	4.2	4.2
Leucine	7.6	7.6	7.7	7.6
Tyrosine	2.2	2.2	1.9	2.2
Phenylalanine	2.8	2.8	2.8	2.8
Histidine	1.6	1.6	1.6	1.6
Lysine	7.7	7.8	7.8	7.8
Arginine	4.0	3.9	4.0	4.0

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FEEDING HABITS OF STOMIATOID FISHES FROM HAWAIIAN WATERS

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ABSTRACT

Stomachs were examined from over 2,800 specimens of stomiatoids collected near Hawaii. Small *Vinciguerria nimbaria* ate mostly small copepods and ostracods, while large fish appeared to switch to large amphipods and small euphausiids. The remaining planktivorous species, sternoptychids and small gonostomatids, fed primarily on large calanoid copepods and small euphausiids. All of these appeared to feed by active, visual searching, and preferred prey were probably more visible than other zooplankton in appropriate size ranges. Diets and preferences of the planktivorous stomiatoids were similar to or identical with those of one or more species of myctophids which share the same habitat. The large gonostomatids ate micronekton but appeared to feed in the same manner as the small individuals and species.

The species from six other families, which appear to be morphologically adapted to ingest relatively large prey, did in fact feed mostly on prey 20% of their body length or longer. Only two species ate zooplankton as well. Most species with chin barbels were nearly or exclusively piscivorous, and those without barbels ate few or no fish. The barbel and analogous structures appear to be used primarily to attract and aid in the capture of relatively large fish. Apparent preferences for certain types of prey by the piscivorous species indicate that interspecific differences in barbel features are related to dietary specialization. Based on feeding incidence and estimates of stomach evacuation time, the piscivorous stomiatoids appear to consume a large fraction of the standing crop of planktivorous fishes each year.

Stomiatoid fishes are important components of the micronekton in most tropical and temperate oceanic areas (e.g., Maynard et al. 1975). Most species occur in the upper 1,000 m and undertake diel vertical migrations (Clarke 1974 and others cited therein). They include both small, planktivorous species and generally larger forms with certain morphological features apparently related to capture of relatively large prey.

Little is known of the feeding habits of these fishes and, consequently, of their role and importance in the pelagic food web. Diets of a few planktivorous species have been reported, but usually from few specimens and without identification of prey beyond major taxa. Clarke (1978) showed that some planktivores feed while at depth during the day. Knowledge of the prey of nekton-eating species has consisted mainly of incidental reports scattered throughout the literature rather than systematic investigations of large numbers of specimens.

This paper presents results of examination of stomach contents of over 70 species of stomiatoids from an extensive series of collections near Hawaii in the north central Pacific Ocean. Almost all the species are vertical migrators; the abundant, nonmigrating species of *Cyclothone*, *Sternoptyx*, and *Argyropelecus* (which are the subjects of separate studies by other investigators) are not included. Diets of the planktivorous species are compared with estimates of prey abundance in appropriate depth ranges in order to determine whether composition and apparent preference are similar to those of cooccurring, nonstomiatoid planktivores which feed in the upper layers at night (Clarke 1980). Data from the nekton-eating stomiatoids allows consideration of preference, feeding methods, and the impact of these predators on the planktivorous micronekton in the community.

METHODS

Specimens for this study were collected ca. 20 km west of the island of Oahu, Hawaii (ca. lat. 21°20-30'N, long. 158°20-30'W) in waters 2,000-4,000 m deep. Previous studies in this area have considered the vertical distribution and certain other aspects of the ecology of stomiatoids (Clarke 1974) and the feeding chronology of five species (Clarke 1978). Other investigations in the

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area have been summarized by Maynard et al. (1975).

Over 2,800 specimens of nine families were examined. Based upon preliminary results, morphology, and the literature, the species were separated into two groups, each of which was treated differently. Members of the Photichthyidae, Sternoptychidae, and Gonostomatidae were considered planktivores; and those of the Astronesthidae, Chauliodontidae, Idiacanthidae, Melanostomiatidae, Stomiatidae, and Malacosteidae as nekton-eating species.

All specimens of planktivorous species were taken with a 3 m Isaacs-Kidd midwater trawl which terminated in a 1 m diameter cone of ca. 3 mm mesh netting with a ca. 2 l nonfiltering cod end bucket. Towing procedures were the same as described in Clarke (1980). The trawl was lowered to a given depth as rapidly as possible, towed for 2-3 h at ca. 2 m/s, and retrieved as rapidly as possible. A time-depth recorder of the appropriate range was attached to the trawls; depth records were accurate to 2-4% of the depth fished. In addition to night tows at 70-170 m described in Clarke (1980), specimens were also taken from day tows at 400-800 m and night tows at 225-250 m made in September 1973 and November 1974 (Table 1). During some of the deeper tows, the trawl changed depth by as much as 50-100 m during the "horizontal" portion of the tow.

Since the most abundant planktivores were known to feed during the day (Clarke 1978), zooplankton were sampled at 400-500 m during the day (Table 1) with opening-closing 70 cm diameter bongo nets (505 μm mesh). The nets were lowered closed, opened for 0.5-1 h at ca. 1 m/s ship's speed, then closed, and retrieved. Time-depth recorders attached to the nets indicated vertical movement of up to 100 m during the open portions of the tows. Volume sampled by each net was estimated from the mouth area, duration of the open portion of the tow, and an estimated speed of 1 m/s.

All material was preserved immediately after capture and held in ca. 4% formaldehyde/seawater. Except for certain trawl samples where large numbers of *Vinciguerria nimbaria* were caught and only individuals with obviously full stomachs were selected, all specimens of each species considered were measured (standard length, SL, to the nearest millimeter) and stomachs examined. Intact prey items were identified, counted, and measured to the nearest 0.1 mm (prosome length for copepods, total length without telson for malacostracans, and total length or maximum dimension for other prey). Identifiable remains among partially digested material were recorded. Any remains of chaetognaths (the only gelatinous prey found) were counted as intact since they are probably degraded much more rapidly than other prey types.

Items in the mouth or esophagus were not counted; their limbs and bodies were not compressed, indicating that they had been taken after capture. Otherwise, there was no evidence of postcapture ingestion by the fishes. Most prey types found intact in the stomach were also recorded as digested remains that had almost certainly been eaten well before capture, and, conversely, several types of abundant zooplankton were rarely or never found in the stomachs, as would be expected if the fish were feeding indiscriminately in the net. There was no evidence that food was regurgitated during or after capture; I found no everted stomachs and no digested remains in the esophagus.

Zooplankton from the bongo net samples were counted from either the entire sample (euphausiids and other relatively large types) or 1/16-1/32 aliquots taken with a Folsom plankton splitter. For both plankton and intact prey items, euphausiids and most copepods (with the exception of unidentifiable copepodites, which were fairly common in all the plankton samples) were identified to species. Ostracods (mostly *Conchoecia*

TABLE 1.—Dates, local (Hawaiian Standard) times, and depths of tows with 3 m Isaacs-Kidd midwater trawl and 70 cm bongo plankton nets off Oahu, Hawaii. Times for trawls are for the period at depth; total times including descent and ascent are in parentheses. Times for bongos are for the open period only. Depth figures are the ranges during "horizontal" portions of tow or modal depth if the range was <20 m.

Date	Time	Depth (m)
Trawls:		
25 Sept. 1973	1523-1723 (1500-1750)	400
9 Nov. 1974	1540-1740 (1535-1802)	400-450
25 Sept. 1973	0748-0954 (0721-1028)	450-500
25 Sept. 1973	1148-1348 (1115-1435)	525
11 Nov. 1974	0818-1118 (0736-1154)	550-600
9 Nov. 1974	0808-1108 (0730-1132)	550-650
26 Sept. 1973	0820-1020 (0742-1120)	600
9 Nov. 1974	1230-1430 (1155-1500)	600-650
12 Nov. 1974	0756-1000 (0722-1100)	650 (briefly to 800)
26 Sept. 1973	1227-1427 (1142-1550)	700-800
10-11 Nov. 1974	2303-0100 (2250-0115)	250
11 Nov. 1974	0155-0505 (0145-0515)	225
Bongos:		
14 Sept. 1973	0930-1033	400-425
14 Nov. 1974	0808-0908	400-425
14 Sept. 1973	1103-1135	425-525
14 Sept. 1973	1241-1311	550

spp.) and amphipods were not further identified, and other prey types were identified only to major taxa. Prey types of the same genus or of similar size, pigmentation, etc. were often lumped for convenience of presentation of results. Densities of zooplankton (Table 2) were calculated from the counts (corrected for any subsampling) and estimated volumes filtered; however, since these are based on so few samples, they can be considered as only rough estimates of prey abundance at the depths where the fishes were caught. Furthermore, the densities of types under 1.0 mm long are underestimated due to mesh escapement; for most of these, densities are probably about 4-5 times higher than estimated from the samples (Clarke 1980).

The nekton-eating species were much less abundant than the planktivores, and their feeding incidence and number of prey per fish were lower; consequently, in order to gather as much data as possible I examined specimens from a wide variety of trawl samples taken between 1969 and 1978. These included both horizontal and oblique samples in the upper 1,200 m—mostly either above 350 m at night or deeper during the day. Almost all were taken with a 3 m Isaacs-Kidd trawl towed at ca. 2 m/s. The terminal section was of fine (333 μm) plankton mesh for about two-thirds of the samples. For a few rare species I also took material from collections with a 5 m Isaacs-Kidd, a 3 m Tucker, or a 2/3 Cobb pelagic trawl. Data from the more abundant fishes were grouped by arbitrary size classes or by time of capture. For the latter, "day" included all tows started and completed between sunrise and sunset plus a few dusk tows which were completed after sunset but fished at or near the day depths of the fishes. Similarly, "night" included tows taken wholly between sunset and sunrise plus a few dawn tows that fished at or near night depths of the fishes.

Specimens were identified, measured, and classified into one of four categories: Damaged—the stomach ruptured or lost during capture, Empty—stomach completely empty or with only a trace of unidentifiable remains, Remains—prey completely disintegrated but identifiable to major taxon, Intact—prey in one piece or a few large pieces. Sizes (standard length of fishes, length without telson of crustaceans, and mantle length of squids) of all intact prey items were recorded. Depending upon size of the item and degree of digestion, the accuracy of these measurements was an estimated ±1-5 mm. Relative length of the prey items, as percentage of standard length of the predators, was used for presentation. Intact crustaceans and many of their remains could be identified to genus or species, but only a fraction of the intact fishes could be unquestionably identified. Where a fish prey could not be identified positively, a probable identification could be often given based on a process of elimination. Because of their photophores, myctophids and some stomiatoids could be identified as such at more advanced stages of digestion than other fishes; in most cases where an item was clearly not a myctophid, it was in good enough condition to be more precisely identified.

There was little evidence of postcapture ingestion of large items. A few very fresh items, i.e., those without a coating of stomach mucus or with the limbs not flattened against the body, were not counted. Most of these items were still partly in the esophagus and were usually types not found as digested remains in the same predator species, e.g., a euphausiid in an otherwise piscivorous species. As with the planktivores, there was no evidence of postcapture regurgitation of prey by nekton-eating species.

Most of the nekton-eating species proved to eat only small nekton (prey $\geq$10 mm long). Zooplankton (usually copepods) were very rarely found in their stomachs—always in near-perfect condition and never as digested remains. Certain species of these fishes, however, appeared to eat both small and large prey, and zooplankton were routinely found in their stomachs. In spite of the fact that many specimens of these species were taken by trawls with a fine mesh terminal section, there was little evidence that the data were biased by postcapture ingestion. As with the strictly planktivorous species, the types of prey found intact included only a narrow range of the types collected in the cod end of the trawl rather than a mixture as would be expected from indiscriminate ingestion in the net, and digested remains of the same types of prey were also recorded for these species. Finally, as will be shown below, the incidence of small items in the stomachs decreased with size of the fish; this would not be expected if these species were for some reason prone to ingestion after capture.

(At towing speeds of less than ca. 1.5 m/s, postcapture ingestion of both large and small items appears to be a serious problem. During the course of this study, I examined specimens from several tows taken at 1.0-1.5 m/s. Zooplankton—

TABLE 2.—Estimated densities of prey types from four plankton tows taken at 400-550 m during the day off Oahu, Hawaii. Data in the third column is from a tow taken in November 1974, the others from September 1973 (see Table 1). A "+" indicates present, but density <0.005/m^3. Except for the *Pleuromamma* spp., identifiable copepodites—usually stage V's—are included with adults.

Prey type	Depth of tow (m)	Density (No./m^3) 400-425	400-425	425-525	550
Copepods:					
Neocalanus spp.		0.05	0.02	0.12	0.07
Nannocalanus minor		0.01	—	—	0.07
Rhincalanus spp.		0.01	—	0.01	—
Eucalanus spp.		0.73	0.60	—	—
Clausocalanus spp.[1]		0.13	0.09	0.05	0.02
Pseudocalanidae[1]		0.57	0.69	0.17	—
Gaetanus/Chiridius spp.		1.18	0.60	0.14	0.07
Aetideidae	<2.0 mm	0.60	0.55	1.49	0.14
	2.0-2.9 mm	—	0.16	0.13	0.23
	≥3.0 mm	—	—	0.03	0.39
Euchaeta media		0.15	0.53	0.40	—
Euchaeta spp.		0.02	0.05	—	0.02
Scottocalanus spp.		—	—	0.11	0.21
Lophothrix spp.		0.01	—	0.02	0.05
Scolecithricidae	<1.0 mm[1]	0.44	0.35	0.19	0.12
	1.0-1.5 mm	0.61	1.96	2.32	1.52
	>1.5 mm	—	—	0.10	0.49
Metridia spp.	≤1.3 mm	0.33	0.05	0.23	0.39
	>1.3 mm	—	—	—	0.02
Pleuromamma xiphias		—	—	0.51	2.08
Pleuromamma xiphias CV		0.47	1.09	0.17	0.16
Pleuromamma abdominalis		0.60	1.99	0.21	0.16
Pleuromamma abdominalis CIV, V		1.84	1.06	0.51	—
Pleuromamma gracilis		2.18	2.01	0.66	0.02
Pleuromamma gracilis CV		0.13	0.05	0.02	0.05
Lucicutia spp.	≤1.3 mm	0.13	0.02	0.05	0.23
	>1.3 mm	—	—	0.04	0.12
Heterorhabdus papilliger		0.27	0.23	0.11	—
Heterorhabdus spp.		0.12	0.14	0.06	0.07
Heterostylites sp.		—	—	0.02	—
Haloptylus sp.		0.02	—	—	—
Augaptilidae		0.10	0.51	0.38	0.14
Arietellus sp.		—	—	0.01	—
Candacia spp.	≤1.5 mm	0.03	0.07	0.01	—
	>1.5 mm	—	—	0.03	0.14
Acartia spp.[1]		—	—	0.01	0.07
Unident. calanoid		0.72	2.08	0.55	1.04
Oithona spp.[1]		0.15	0.14	0.04	0.02
Oncaea mediterranea[1]		0.06	0.10	0.02	0.02
Oncaea conifera[1]		0.06	0.05	0.09	0.05
Oncaea spp.	≤0.6 mm[1]	0.21	—	0.27	—
Corycaeus spp.		0.01	—	0.04	—
Aegisthes spp.		0.16	0.02	0.13	0.09
Copilia spp.		0.07	—	—	—
Monstrilla sp.		0.01	—	—	—
Mormonilla sp.		—	—	0.04	0.07
Amphipod	<2.0 mm	+	+	+	—
	2.0-2.9 mm	+	+	+	+
	≥3.0 mm	0.01	0.01	0.04	0.01
Ostracod	≤1.0 mm[1]	0.16	0.16	0.11	0.05
	1.1-1.9 mm	0.30	0.12	0.26	0.11
	≥2.0 mm	0.01	—	0.04	0.02
Euphausiids:					
Euphausia spp.		2.30	0.04	0.40	0.02
Stylocheiron spp.		0.02	0.01	+	—
Nematoscelis spp.		0.03	0.01	0.12	0.02
Thysanopoda aequalis		0.01	0.01	0.02	+
Thysanopoda spp.		0.01	+	0.01	0.01
Nematobrachion spp.		+	+	+	—
Euphausiid larva		0.01	0.03	—	+
Isopod		+	—	+	—
Megalops		—	—	+	—
Cyprus		0.16	0.06	0.03	+
Polychaete		0.01	0.01	+	—
Chaetognath		0.76	0.36	0.23	0.06
Pteropod		+	0.01	+	—
Fish larva		—	—	+	0.01

[1]Densities seriously underestimated due to mesh escapement.

up to 10-12 assorted copepods and ostracods, all apparently recently ingested—were found in several stomachs of fishes that otherwise had eaten only relatively large items. I also found several apparently freshly ingested euphausiids and sergestid shrimps in stomachs of fishes that otherwise appeared to be strictly piscivorous. Specimens from these slow tows were not included in the data presented here.)

Estimates of biomass and relative abundance of vertically migrating fishes in the study area and of feeding incidence of the nekton-eating stomiatoids were made from catches of a series of oblique 3 m Isaacs-Kidd trawl tows taken at approximately monthly intervals between August 1977 and November 1978. A time-depth recorder and a flowmeter were mounted on the trawl for all tows. All fishes were identified, species were grouped by taxa and known or probable feeding habits, and wet weights of each group determined for each sample. All nekton-eating stomiatoids from the series were examined and are included in the results below.

The 58 night tows in this series fished between the surface and ca. 350 m and covered the nighttime depth range of all vertically migrating species. The relative abundances of the different taxonomic and trophic groups were calculated based upon total numbers from all the night tows. Biomass (wet weight) per unit area of each group was calculated as in Maynard et al. (1975) for each sample. The overall mean of all samples and all seasons was used as the estimated average biomass. The 28 day tows covered the day depth ranges of the vertically migrating species (ca. 350-1,000 m), but for various reasons it was not possible to reliably estimate volume filtered (and therefore biomass per unit area) from these tows. The numbers of nekton-eating stomiatoids and of prey species in the catch and the numbers of prey found in the stomachs of the stomiatoids from both day and night tows were used to estimate feeding incidence relative to the numerical standing crop of prey species.

RESULTS

Photichthyidae

Vinciguerria nimbaria (Table 3) from three samples within its day depth range were divided into two size groups (16-25 mm and over 25 mm SL). Catches of three of the six size-depth groups were high, and only fish with visually apparent full stomachs were selected for examination (Table 3, columns 3, 5, 6). All fish of the other groups were examined, but total numbers of intact prey were still quite low for these.

Overall the most frequent items in the stomachs were small copepods and ostracods. *Oncaea* spp. were the dominant prey in most size-depth groups, and in all samples *Oncaea*—especially the small forms—were more frequent in the diets of the smaller fish than in those of the large. Beyond this, however, the diet composition varied between groups without much apparent relation to size or depth, e.g., *Clausocalanus* spp. and *Pleuromamma gracilis* were important fractions of the prey of the small fish from 400 m and both size groups from 450 to 500 m; candaciids and *Scolecithrix danae* were taken by most groups, but decidedly more frequently (as percentage of prey items) by the large fish from 400 m; the frequency of ostracods varied among the groups from 3% to 42% of the total items.

Some of this variability was undoubtedly a consequence of small sample sizes from three groups, but part resulted from large numbers of certain prey types occurring in only one or a few of the fish from a given size-depth group. Examples include (see appropriate column of Table 3): All 7 *P. gracilis* from 1 of 6 fish with prey (column 1); all 5 amphipods from 1 of 3 fish (column 2); 4 of 5 *Undinula* spp. from 1, 4 of 5 *Sapphirina* spp. from another, and all 11 pelecypod larvae from another out of 18 fish (column 3); 13 of 41 *Clausocalanus* spp. in 1 and 34 of 73 *P. gracilis* in 3 others out of 20 fish (column 5); 14 of 15 *Scolecithrix danae* in 1 and 24 of 34 *P. gracilis* in 2 others out of 9 fish (column 6). The presence or absence of only one or two fish such as these had an important effect on percentages of certain items in the estimated diet of a size-depth group.

Vinciguerria nimbaria over 30 mm SL had eaten considerably larger items more frequently than smaller fish. The only large day-caught specimen (37 mm) contained remains of another fish, a 3.0 mm amphipod and two *Nematobrachion* spp., each ca. 15 mm long. Ten specimens over 30 mm were taken in a night tow at 70 m. Most items in the stomachs of these fish were on the borderline between "intact" and "remains" and difficult to count similarly to those from the day specimens, but it was clear that euphausiids—mostly *Stylocheiron* spp.—were the most frequent items and that small copepods were much less important than in the smaller fish. Remains of six to nine *Stylocheiron* each were found

TABLE 3.—Numbers of intact items of different prey types from stomachs of *Vinciguerria nimbaria* and *V. poweriae* from several depths and times. Remains of types not found intact are denoted by "r"; in column seven (*V. nimbaria*, Night, 70 m), numbers of nearly intact remains (see text) are given in parentheses.

	V. nimbaria							*V. poweriae*	
	Day						Night	Day	Night
Depth (m)	400		400-450		450-500		70	400-300	225-250
Size (SL, mm)	17-25	26-30	16-24	26-30	17-25	26-30	31-39	23-29	20-34
No. examined	14	8	18	13	20	9	10	11	16
No. w/intact prey	6	3	18	4	20	9	0	8	7
No. of intact prey	54	33	270	31	437	192	0	57	17
No. of prey type:									
Neocalanus spp.	—	—	—	—	1	1	r(4)	—	—
Nannocalanus minor	—	—	—	—	—	1	—	—	—
Undinula spp.	—	—	5	—	1	1	—	—	—
Clausocalanus spp.	3	—	1	—	41	13	—	—	—
Euchaeta spp.	—	1	—	—	—	4	r(2)	—	—
Aetideidae	—	—	—	—	—	2	r(1)	—	—
Scolecithrix danae	—	5	3	1	2	15	—	—	—
Scolecithricidae ≤1.0 mm	1	—	—	1	2	2	—	—	—
Scolecithricidae >1.0 mm	—	1	—	—	5	1	—	2	—
Pleuromamma abdominalis	—	—	—	r	3	1	—	1	—
Pleuromamma spp. CIV, CV	—	—	1	—	8	2	—	—	—
Pleuromamma gracilis	7	r	5	1	73	34	—	—	r
Lucicutia spp. ≤1.3 mm	3	r	3	—	20	9	—	—	1
Heterorhabdus spp.	—	—	1	—	2	1	—	—	—
Augaptilidae	—	—	—	—	—	1	—	—	—
Candacia spp.	1	1	2	—	4	6	r(1)	3	r
Paracandacia spp.	—	7	2	—	1	3	r(13)	1	2
Unident. calanoid	—	1	—	—	6	2	r(5)	—	—
Corycaeus spp.	—	1	10	—	11	1	r(1)	—	—
Oncaea mediterranea	9	2	66	6	82	13	r(2)	6	5
Oncaea conifera	10	2	43	4	55	17	—	7	—
Oncaea venusta	1	—	19	1	7	4	—	3	3
Oncaea spp. ≤0.6 mm	13	2	29	—	67	24	—	3	1
Sapphirina spp.	—	—	5	1	—	1	r(1)	—	—
Aegisthes spp.	—	—	—	—	—	1	—	—	—
Euphausia spp.	—	r	r	—	6	2	—	2	—
Stylocheiron spp.	—	—	—	—	—	r	r(28)	r	r
Nematobrachion spp.	—	—	—	—	—	—	—	1	r
Euphausiid larva	—	—	1	—	3	4	r(1)	—	—
Caridean larva	—	1	—	—	—	1	—	—	—
Amphipod <2.0 mm	—	1	4	—	2	—	—	1	—
≥2.0 mm	—	4	3	1	4	4	r(46)	—	—
Ostracod ≤1.0 mm	2	—	27	4	16	9	—	5	2
>1.0 mm	4	1	20	9	14	8	r(9)	16	3
Gastropod larva	—	—	8	—	1	1	—	6	—
Pelecypod larva	—	—	11	—	—	—	—	—	—
Heteropod (*Atlanta* spp.)	—	1	1	—	—	—	—	—	—
Chaetognath	—	1	—	—	—	1	r(1)	—	—
Fish larva	—	1	r	2	—	2	r(2)	r	r

in four of the large *V. nimbaria*. Amphipods were also apparently important items in the diet of these large fish, but similar to the above examples, about 38 of the approximately 46 amphipods recorded were eaten by only 2 of the 10 fish.

Vinciguerria poweriae was taken in small numbers in the same day tows as *V. nimbaria* and at night at 225-250 m (Table 3). Both the incidence of fish with intact prey and the number of prey per fish were lower at night, indicating that, like *V. nimbaria* (Clarke 1978), *V. poweriae* feeds during the day. The items and remains found in stomachs of both groups indicate that *V. poweriae's* diet is generally similar to that of *V. nimbaria* of the same sizes. The lower percentages of *Oncaea* spp., higher percentages of ostracods, and less diversity may have been an artifact of small sample size.

Sternoptychidae

Valenciennellus tripunctulatus and *Danaphos oculatus* (Table 4) were taken in day tows with and slightly deeper than the *Vinciguerria* spp. The small *Valenciennellus tripunctulatus*—mostly from the shallower tows—had eaten some *Oncaea* spp., ostracods, and small (1.0-1.5 mm) calanoids, but most of their prey and all of those of the larger fish were medium to large calanoids. Few prey were found in *D. oculatus*, but with the exception of a small scolecithricid and remains of an ostracod, all were large calanoids.

Gonostomatidae

The diet of *Gonostoma atlanticum* (Table 5) from day tows consisted of essentially the same

TABLE 4.—Numbers of intact prey from stomachs of *Valenciennellus tripunctulatus* from day samples at four different depths and of *Danaphos oculatus* combined from four different day samples. Remains of types not found intact are denoted by "r."

	Valenciennellus tripunctulatus				*Danaphos oculatus*
Depth (m)	400	400-450	450-500	525	400-600
Size (SL, mm)	22-30	23-29	28-31	29-34	28-40
No. examined	11	10	3	4	21
No. w/intact prey	11	10	3	4	10
No. of intact prey	84	44	7	34	21
No. of prey type:					
Neocalanus spp.	—	1	—	—	—
Eucalanus spp.	3	—	—	1	—
Clausocalanus spp.	4	1	—	1	—
Aetideidae <2.0 mm	4	—	—	2	3
>2.0 mm	10	3	1	—	8
Euchaeta media	12	4	2	6	5
Scolecithricidae <1.0 mm	4	2	—	—	1
≥1.0 mm	3	1	1	9	—
Pleuromamma xiphias	11	11	1	12	3
Pleuromamma xiphias CV	9	1	—	—	—
Pleuromamma abdominalis	3	2	2	1	—
Pleuromamma abdominalis CV	1	—	—	—	—
Pleuromamma gracilis	6	—	—	—	—
Heterorhabdus papilliger	4	1	—	—	—
Heterorhabdus spp.	2	—	—	—	—
Candacia longimana	—	—	—	1	1
Oncaea conifera	2	5	—	—	—
Oncaea spp. ≤0.6 mm	—	1	—	—	—
Corycaeus spp.	—	1	—	—	—
Ostracod ≤1.0 mm	—	2	—	—	—
1.1-1.9 mm	1	3	—	—	r
Unident. calanoid	5	4	—	1	—
Chaetognath	—	1	—	—	—

TABLE 5.—Numbers of intact prey from stomachs of four species of gonostomatid fishes taken day and night and combined from two or more samples within given depth ranges. In this table, a few stage V copepodites of *Pleuromamma xiphias* and *P. abdominalis* are included with adults. Prey types not found as intact items are denoted by "r." Additional remains from fish of column seven (225-250 m depth) included a penaeidean shrimp and a large *Metridia* sp. Data for *Gonostoma elongatum* and *G. ebelingi* over 120 mm SL are in Table 6.

	Gonostoma atlanticum				*Gonostoma elongatum*			*Gonostoma ebelingi*		*Diplophos taenia*	
	Day		Night		Day	Night		Day		Day + night	
Depth (m)	400-525		170-250		400-800	110-170	225-250	400-500	525-650	400-650 + 90	
Size (SL, mm)	22-45	46-65	25-44	46-54	34-78	29-88	93-120	34-77	94-117	53-93	103-171
No. examined	34	29	26	9	24	15	17	9	21	9	14
No. w/intact prey	25	21	7	4	6	9	2	7	4	8	9
No. of intact prey	74	46	10	5	22	18	3	20	9	13	19
No. of prey type:											
Neocalanus spp.	—	—	—	—	1	—	—	—	—	1	—
Undinula sp.	—	—	—	—	—	—	—	—	—	1	—
Eucalanus spp.	1	—	—	—	—	—	—	—	—	—	—
Aetideidae	2	2	—	1	4	—	—	2	3	—	—
Euchaeta media	r	1	—	1	—	—	—	1	—	—	—
Scottocalanus spp.	r	2	1	2	r	—	—	—	4	—	—
Amallothrix spp.	2	1	—	—	—	—	—	—	—	—	—
Pleuromamma xiphias	33	10	1	—	11	15	2	5	r	2	2
Pleuromamma abdominalis	8	3	2	—	—	1	—	—	—	4	—
Pleuromamma gracilis	—	1	—	—	—	—	—	—	—	—	—
Lucicutia spp.	1	—	1	—	—	—	—	—	—	—	—
Candacia longimana	6	3	1	r	2	—	r	r	—	—	—
Unident. calanoid	1	—	2	1	—	—	—	—	—	—	—
Oncaea spp.	3	—	—	—	1	—	—	6	—	—	—
Euphausia spp.	13	14	2	—	—	1	r	1	—	5	4
Stylocheiron spp.	2	—	—	r	r	r	r	r	—	—	—
Nematoscelis spp.	—	6	—	—	—	—	—	—	1	—	—
Nematobrachion sp.	—	—	—	—	—	—	1	—	—	—	—
Thysanopoda aequalis	—	3	—	r	1	—	—	1	—	—	2
Thysanopoda spp.	—	—	—	—	—	—	r	—	—	r	1
Euphausiid larva	—	—	—	—	—	—	—	—	—	—	1
Ostracod	1	—	—	—	—	1	—	4	1	r	—
Amphipod	—	—	—	—	2	—	r	—	—	—	7
Fish	1	—	—	—	r	—	r	r	—	—	2

types of copepods eaten by the sternoptychids plus small (8-12 mm) species of euphausiids. The euphausiids were over twice as frequent and, among the copepods, *P. xiphias* and *P. abdominalis* much less important in the diet of the larger of the two size groups of fish. *Gonostoma atlanticum* appears to feed by day (Clarke 1978); as expected, the remains and few intact prey items found in night-caught specimens were similar to those from day-caught fish.

Gonostoma elongatum were divided into three size groups. Specimens <90 mm SL from both day and night tows (Table 5) contained mostly large copepods, the majority of which were *P. xiphias*. Euphausiids or their remains were found in several specimens; only one, a *Thysanopoda aequalis*, was over 10% of the fish's length. Intermediate-sized *G. elongatum* (93-120 mm SL) were taken only at night, and most stomachs contained only digested remains. The frequency of euphausiids in the diet appeared higher than in the small fish, and one plus the remains of two others were over 10% of the fish's length. *Gonostoma elongatum* over 120 mm (Table 6) had eaten large prey in all but two cases. Relative sizes of most measurable items were about 10%, but values ranged from 3.8% to 27% (excluding two copepods and a somewhat suspicious pyrosome). Penaeidean shrimps and euphausiids were the most frequent items and remains, but fish were taken by several and squid by two of the large specimens.

Limited data for *G. ebelingi* and *Diplophos taenia* indicated that both diet and differences between size groups were similar to those of *G. elongatum*, but there were some differences in important prey types. Data for *G. ebelingi* came exclusively from day tows. Small fish (Table 5) had eaten small zooplankton—*Oncaea* spp. and ostracods—as well as the larger *P. xiphias* and euphausiids; the intermediate-sized individuals had eaten only large zooplankton. The largest fish (Table 6) had eaten only fish and crustaceans over 10 mm long; the relative sizes of intact items were 11-24%. *Diplophos taenia* (Table 5) were mostly from day tows. Small fish had eaten medium to large copepods and *Euphausia* spp. The large fish contained few copepods or their remains; most prey were small euphausiids or the large (5-6 mm) amphipod *Vibilia* spp. The two largest fish examined had eaten myctophids. One of the myctophids (*Lampanyctus* sp.) and a *T. tricuspidata* were relatively large (29 and 22%, respectively), but all other items were <10%.

Astronesthidae

Astronesthes indicus under 60 mm SL fed mostly on copepods and ostracods (Table 7). Small prey types, especially *Oncaea* spp., were more frequent in diets of fish under 30 mm SL. Of the two species of scolecithricid copepods eaten, the smaller *Scolecithrix danae* (ca. 1.5 mm prosome length) was more frequent in the diet of the fish under 30 mm than in the 31-60 mm fish, but the larger *Scottocalanus* spp. (over 3 mm PL) were more frequent in the larger fish. Euphausiids were only slightly more frequent in the diet of the 31-60 mm fish than in that of the smaller ones; remains of euphausiids, including five in one fish, were found only in the 31-60 mm group. The few individuals over 60 mm SL (Table 6) were mostly empty; only a myctophid and fish remains were found.

The smallest individual of *A. "cyaneus"* (15 mm SL) had eaten small zooplankton, but those 20-47 mm SL (Table 6) had eaten only *Euphausia* spp.—some up to almost one-half their own length. Fish remains were found in two of the three larger fish examined. The small and intermediate-sized *A. splendidus* had eaten a few copepods and a small euphausiid, but all other prey of all sizes were relatively large—an average of 41% of SL—and all but two were fish (Table 6). Small *A. "similis"* (Table 6) contained only fish remains; the large individuals contained fish and a single euphausiid whose relative length was considerably less than those of the fishes eaten. (See Clarke 1974, regarding differences between the two provisionally identified species and *A. cyaneus* and *A. similis*.)

The items found in *Heterophotus ophistoma* (Table 6) were unique in several respects, but the significance of these cannot be assessed from the insufficient data here. One of the small specimens contained squid remains—otherwise found in only two specimens of *G. elongatum*. The four large specimens contained two sergestids, a *Sternoptyx* sp.—the only nonmigrating fish found in any stomiatoid, and remains of a *Parapandalus* sp.—the only adult caridean shrimp found. All of these items were relatively smaller than prey of most other nekton-eating species.

Chauliodontidae

Chauliodus sloani (Table 6) had eaten mostly fish; only those <120 mm had taken crustaceans—mostly euphausiids—frequently. The

TABLE 6.—Summary of stomach analyses for nekton-eating stomiatoids. See text for definition of categories. Under "Time" (first column): D = day, N = night, B = both combined. Under "Remains recorded" (last column): e = euphausiid, s = sergestid, c = unidentifiable crustacean, m = myctophid, f = unidentifiable fish, sq = squid. See text for explanation of groups of unidentified *Eustomias* spp.

Family/species	Time	SL (mm)	No specimens (damaged)	% of undamaged specimens			Relative lengths of prey in % of predator SL (No. of items)		Remains recorded
				Empty	Remains only	Intact items	Fish	Crustaceans	
Gonostomatidae:									
Gonostoma elongatum	D	138-207	11(0)	64	9	27	13-20(2)	10-13(3)	e,sq[1]
	N	126-210	10(0)	10	40	60	13-17(2)	6-27(6)	e,c,f,sq[2]
Gonostoma ebelingi	D	121-143	19(0)	58	32	11	—	11-24(3)	e,c,m,f
Astronesthidae:									
Astronesthes indicus	B	64-152	20(2)	83	11	6	29(1)	—	f
Astronesthes "cyaneus"	B	15-47	30(0)	60	23	17	—	24-48(6)	e,c[3]
	B	114-164	3(0)	33	67	0	—	—	m,f
Astronesthes splendidus	B	22-39	31(1)	53	23	23	32-63(5)	31-41(2)	e,m,f[4]
	B	41-58	17(0)	76	6	18	41-44(2)	—	c,m,f[5]
	B	66-95	14(0)	57	7	36	21-64(5)	—	m
Astronesthes "similis"	B	23-68	27(1)	73	27	—	—	—	m,f
	B	98-122	5(0)	40	20	40	25-41(2)	8(1)	f
Heterophotus ophistoma	B	35-70	8(1)	86	14	—	—	—	sq
	B	141-320	4(0)	25	25	50	7(1)	6-11(2)	c
Chauliodontidae:									
Chauliodus sloani	D	20-60	43(4)	62	18	20	33-45(7)	20(1)	e,m,f
	N	20-60	57(9)	58	23	19	31-63(6)	10-20(2)	e,m,f
	D	61-120	12(2)	50	20	30	21(1)	11-16(3)	e,f
	N	61-120	33(9)	54	25	21	22-42(6)	—	m,f
	D	121-255	24(6)	44	22	33	14-33(5)	13(1)	f
	N	121-232	23(11)	50	25	25	14-19(3)	—	c,f
Idiacanthidae:									
Idiacanthus fasciola	D	50-100	55(25)	90	10	—	—	—	m,f
	N	50-100	73(24)	88	4	8	16-22(4)	—	f
	D	101-200	38(6)	72	19	9	17-20(3)	—	m,f
	N	101-200	57(8)	78	14	8	9-20(4)	—	f
	D	201-375	37(1)	75	14	11	13-23(4)	—	f
	N	201-372	102(7)	84	6	9	10-23(8)	4-8(2)	f
Melanostomiatidae:									
Thysanactis dentex	D	121-167	29(0)	86	—	14	30-48(4)	—	—
	N	121-174	51(5)	67	13	20	21-42(5)	14-29(3)	f[6]
Eustomias bifilis	D	50-90	40(5)	91	—	9	19-20(3)	—	—
	N	50-90	95(2)	85	4	11	17-47(10)	—	m,f
	D	91-165	36(5)	74	13	13	8-21(4)	—	m,f
	N	91-170	60(2)	91	5	3	15-33(3)	—	f
Eustomias enbarbatus	B	56-219	26(3)	78	13	9	16-41(2)	—	f
Eustomias spp. (3,low)	B	50-160	46(4)	79	7	14	17-32(6)	—	f
Eustomias longibarba	B	66-152	50(3)	79	9	11	24-42(5)	25(1)	f
Eustomias gibbsi	B	61-141	35(3)	91	3	6	34-37(2)	—	f
Eustomias spp. (3,hi)	B	55-161	134(7)	83	9	8	17-34(10)	—	f
Eustomias "silvescens"	B	60-180	32(1)	68	6	26	23-48(8)	—	f
Eustomias spp. (2)	B	60-161	152(0)	80	8	12	17-76(18)	14(1)	f
Bathophilus kingi	B	24-140	3(2)	76	17	7	23-40(3)	—	f
Bathophilus spp.	B	26-90	27(3)	67	21	12	45-67(3)	—	f
Photonectes spp.	B	22-78	14(2)	42	25	33	34-72(4)	—	f
	B	132-240	10(0)	90	—	10	26(1)	16(1)	—
Leptostomias spp.	B	35-290	31(2)	83	7	10	13-29(3)	—	f
Melanostomias spp.	B	62-165	8(0)	75	12	12	33(1)	—	f
Stomiatidae:									
Stomias danae	B	42-183	12(0)	75	8	17	24-33(2)	—	f
Malacosteidae:									
Aristostomias spp.	B	33-140	25(8)	71	24	6	35(1)	—	m,f
Photostomias spp.	B	29-51	37(6)	68	13	19	—	9-30(4)	s,c
Photostomias sp. 1	B	52-102	73(4)	74	16	10	—	15-28(8)	s,c
Photostomias sp. 2	B	51-90	54(2)	67	21	12	—	29-42(6)	s,c
Photostomias sp. 2	B	91-140	38(1)	89	8	3	—	30(1)	s,c

Small intact items also recorded:
[1] *Euchirella* sp.
[2] *Pleuromamma xiphias*, caridean larva, pyrosome.
[3] *Oncaea* spp., ostracod.
[4] *P. xiphias*, *P. abdominalis*, euphausiid larva
[5] *P. xiphias*, *Euchirella* sp.
[6] Isopod

fishes eaten by the smallest size group were relatively larger (30-63%) than the fishes from the larger *C. sloani* (14-29% with one exception) or any of the crustaceans (10-20%). Of the 28 fish eaten, 18 were myctophids of at least 5 different genera (*Ceratoscopelus*, *Hygophum*, *Notolychnus*, *Lampanyctus*, and *Triphoturus*); five others were definitely not myctophids and included one and probably a second *Vinciguerria nimbaria* and what was most likely a *Bregmaceros* sp.

TABLE 7.—Summary of stomach analyses of planktivorous sizes of *Astronesthes indicus* and *Thysanactis dentex*. For large prey types, the range of relative lengths in percentage of predator length is given in parentheses after the count. Data for larger fishes of both species are in Table 6.

	Astronesthes indicus				*Thysanactis dentex*			
Size (SL, mm)	15-30		31-60		43-90		91-120	
Time	Day	Night	Day	Night	Day	Night	Day	Night
No. examined (No. damaged)	23(0)	37(1)	43(1)	55(2)	78(1)	104(3)	37(0)	79(5)
Percent undamaged:								
Empty	70	67	86	77	57	44	73	68
Remains only	—	3	2	4	10	19	8	8
Intact items	30	31	12	19	32	38	19	24
Intact large items	4	8	2	9	16	21	16	22
No. of prey type:								
Eucalanus sp.	—	1	—	—	—	—	—	—
Aetideidae	3	—	—	—	8	8	—	2
Scolecithrix danae	3	6	1	2	—	—	—	—
Scottocalanus spp.	—	1	1	4	1	—	—	—
Pleuromamma xiphias	1	—	—	—	24	21	2	13
Pleuromamma abdominalis	—	—	—	—	5	3	—	3
Other calanoid	6	3	—	5	5	3	—	—
Oncaea spp.	16	9	1	4	—	—	—	—
Aegisthes sp.	—	1	—	—	—	—	—	—
Euphausia spp.	1(21)	2(19-35)	1(14)	4(12-30)	2(7-13)	3(10-13)	1(10)	3(10-11)
Nematoscelis sp.	—	—	—	—	—	1(11)	—	—
Thysanopoda aequalis	—	1(21)	—	—	8(12-19)	18(11-19)	1(10)	4(10-13)
Thysanopoda spp.	—	—	—	1(30)	1(24)	3(23)	1(22)	3(21-28)
Euphausiid larva	3	6	1	1	2	1	—	—
Decapod larva	—	1	—	—	—	1	—	—
Sergestes spp.	—	—	—	—	—	2(18-20)	—	1(11)
Ostracod	21	15	14	8	—	1	—	—
Fish	—	—	—	—	2(23-24)	3(15-36)	3(16-43)	7(18-53)

Idiacanthidae

All sizes of *Idiacanthus fasciola* had eaten fish nearly exclusively (Table 6). Of the 23 fish, 15 were myctophids of at least 5 genera (*Bolinichthys, Ceratoscopelus, Diaphus, Lampanyctus,* and *Triphoturus*). Only one of the others, possibly a stomiatoid, was definitely not a myctophid. The largest prey of all sizes of *I. fasciola* were about 20% of the predator's length, but the minimum and average relative size of prey were somewhat higher in the small *I. fasciola*. The only two crustaceans found were intact, but neither appeared to have been very recently ingested. No crustacean remains were found, and the two intact crustaceans were smaller than all (substantially smaller than most) of the fishes eaten. Two other, smaller items—a pyroosome and a copepod—found in *I. fasciola* were not counted because they showed no sign of digestion or compression. Thus *I. fasciola* must have occasionally fed in the net and may have ingested the crustaceans there. Whatever the case, crustaceans are certainly a very minor part of the diet.

Melanostomiatidae

Thysanactis dentex under 120 mm SL had eaten zooplankton as well as large prey (Table 7). The 43-90 mm size group had eaten small euphausiids—mostly *Thysanopoda aequalis* 11-19% of their length—and large, pigmented copepods—mostly *Pleuromamma xiphias*; however, several relatively larger (15-36% of SL) fishes, *Thysanopoda* spp., and sergestids were also found. Fish 91-120 mm had eaten copepods and small euphausiids much less frequently; the bulk of the diet was relatively large fish and crustaceans. With the exception of a single isopod, the items and remains from fish >120 mm (Table 6) included only relatively large prey: other fishes, a large *Thysanopoda* spp., and two sergestids. Of the 24 intact fishes from all sizes of *Thysanactis dentex*, 9 were definitely myctophids of at least 5 different genera (*Bolinichthys, Diaphus, Diogenichthys, Lampadena,* and *Triphoturus*), and 11 were definitely of other families, including 6 *Bregmaceros* spp. and 2 *Melamphaes* spp. Most of the high values of relative size were for the slender *Bregmaceros* spp. The three *B. japonicus* from the 91-120 mm SL *Thysanactis dentex* were 45-53% compared with 11-28% for the remaining fishes and large crustaceans. Among the prey from *T. dentex*, over 120 mm SL, the three *Bregmaceros* sp. (c.f. *B. macclellandi*) ranged from 39 to 42%, while with the exception of an unidentified fish at 48%, the remaining fish prey were 14-32%.

There were approximately 30 species of *Eustomias* in the collections, many of them either

undescribed or of uncertain status. *Eustomias bifilis* was the only one for which large numbers were available, and only 4 others were represented by more than 25 specimens (Table 6). The remaining identifiable species were pooled according to pectoral ray and photophore counts along with specimens whose barbels had been damaged and could not be identified to species. Those designated "3, low" were all damaged specimens with 3 pectoral rays and 15 or fewer VAL and VAV photophores. *Eustomias bifilis* and *E. enbarbatus* were the only other species from the area with the same counts. Those designated "3, hi" included 69 specimens of at least 6 undescribed species and 65 damaged specimens, all with 3 pectoral rays and over 15 VAL and VAV photophores—the same counts as for *E. longibarba* and *E. gibbsi*. Those designated "2" included 6 damaged specimens and 146 others of about 20 species, which, like *E. "silvescens,"* had only two pectoral rays. The 2-rayed species have shorter and generally more ornate barbels than any of the 3-rayed species (cf. illustrations in Morrow and Gibbs 1964).

All prey items and remains from the 3-rayed species with low counts were fish. Of 20 intact items from *E. bifilis*, 11 were the myctophid *Bolinichthys longipes* and 6 were myctophids of at least 3 other genera (*Benthosema, Diogenichthys*, and *Hygophum*). One of the three unidentified items was definitely not a myctophid and was probably a *Howella* sp. The range of relative size of prey (15-34% of SL) was large, but there was no trend with the size of the predator. One and probably both of the intact fish found in *E. enbarbatus* were *Howella* sp. The six intact items from the damaged specimens (most of which were probably the abundant *E. bifilis*) included three *Bolinichthys longipes*, a *Benthosema*, an unidentified myctophid, and an unidentified fish.

The prey of *E. longibarba, E. gibbsi*, and the other species with three pectoral rays and high photophore counts were, with one exception, fish. Of the 17 intact fish, 15 were myctophids including 7 and probably 8 *Bolinichthys longipes* and at least 2 other genera (*Benthosema* and *Ceratoscopelus*). The median relative size of fish prey for these *Eustomias* spp. (25%) was significantly higher ($P<0.05$, Mann-Whitney test, one-tailed probability) than that for the *Eustomias* spp. with three rays and low photophore counts (20.5%). One specimen of *E. longibarba* had eaten a large euphausiid, *Thysanopoda pectinata*.

One of the *Eustomias* spp. with two pectoral rays had eaten a sergestid shrimp, but all other prey of this group were fish. These *Eustomias* spp. appeared to eat fewer and different myctophids than did any of the 3-rayed species. *Eustomas "silvescens"* (cf. fig. 106A in Morrow and Gibbs 1964), the most commonly taken species of this group, had eaten three *Scopelosaurus* spp., three myctophids (two *Bolinichthys longipes* and a *Diaphus*), and two unidentified fish. Stomachs of the remaining species contained a total of 18 intact fish: 12 myctophids, 2 *Howella* sp., and 4 *Scopelosaurus* spp. (plus 2 more of the latter that were too digested to measure). Five and probably six of the myctophids were *Diaphus* spp., and only three and probably four were *B. longipes*. In the 3-rayed species of *Eustomias, Diaphus* was found only once, and *B. longipes* was the most common prey. Although data are too few to be certain, some of the 2-rayed species appeared to have diets that were restricted or included high proportions of relatively rare fishes. For one undescribed form, all four items were *Diaphus* spp.; for another, two out of four were *Howella* sp.; and for a third and fourth, two out of two items and two out of four remains, respectively, were *Scopelosaurus* spp. The median relative size of prey of the 2-rayed species (27%) was significantly ($P = 0.01$) higher than that for the 3-rayed species with low counts, but did not differ from that for the 3-rayed species with high counts.

The two crustaceans recorded from *Eustomias* spp. appear suspicious and indicative of postcapture ingestion, especially since no digested crustacean remains were found in any of the stomachs. The two items showed no obvious signs of having been eaten after capture, but neither were they much digested. The only indirect evidence that these were actual prey items and not eaten in the net is that I have found both crustaceans and their remains in the stomachs of several *E. bulbornatus*, a species which does not occur in the study area. Since at least one species of the genus appears to eat crustaceans, it is possible that others may do so occasionally.

Based upon a limited amount of data (Table 6), the remaining melanostomiatid genera, as well as *Stomias danae* (Stomiatidae) and the *Aristostomias* spp. (Malacosteidae), are piscivorous. All the identifiable fish eaten by these species were myctophids. All three items from *Leptostomias* spp. were *Notolychnus valdiviae*. The relative size of prey of the small *Photonectes* spp. and several of the *Bathophilus* spp. was high—

over 50% in several cases. The only crustacean found was a partially digested penaeidean shrimp, together with a myctophid, in a large *Photonectes* sp.

Malacosteidae

Only 24 items were found in the 100 *Malacosteus niger* examined (Table 8). The most frequent items were copepods; these included some small harpacticoids, but most were large aetideids or scolecithrididds. Similar-sized *Pleuromamma xiphias* were conspicuously absent. Two fish (86 and 93 mm SL) had eaten somewhat larger prey, and remains of relatively large prey were found only in the three largest fish examined. The incidence of intact prey was much lower in the larger of the two size groups.

As indicated in Clarke (1974), two species of *Photostomias* occur near Hawaii; neither is identical with *P. guernei*, the only presently recognized species. The form designated species 1 here matures at about 60 mm SL and grows to ca. 100 mm SL, while species 2 matures at about 120 mm SL and grows to >150 mm SL. Individuals less than ca. 50 mm SL cannot be reliably separated. The data given in Table 6 are limited to specimens that were analyzed after I had learned to separate the species as well as possible; the text below, however, also includes prey identifications and relative sizes from 54 other specimens from earlier collections. These 54 specimens were no longer conveniently available to me after I had learned to separate the species, and could not be identified with certainty from notes taken at the time of examination.

Both species ate crustaceans exclusively, and with few exceptions the prey and identifiable remains were sergestid shrimps, mostly small *Sergestes* spp. Two large individuals of species 2 had eaten *Gennadas* spp., and an unidentified small specimen had eaten a *Nematobrachion*, the only euphausiid found. Aside from the *Gennadas* occurring only in species 2, there was no evidence of difference in diet between the two species. Except for a juvenile shrimp eaten by a small fish, relative length of prey was 15-42% of SL with a median of 28.5%.

TABLE 8.—Summary of stomach analyses of *Malacosteus niger* with list of all items and remains found.

Size (SL, mm)	No. examined (damaged)	% undamaged specimens: Empty	Remains only	Intact items
24-90	44(3)	71	2	27
91-188	56(0)	88	4	9

SL—items or remains:

30	*Undeuchaeta plumosa*
37	*Candacia longimana, Chirundina streetsi*, aetideid CV, copepod remains
61	*Undeuchaeta major*
70	*Oncaea* sp.
70	remains of 3-4 copepods
71	2 *C. streetsi*, 2 *U. major, Euchirella curticauda*
80	2 *C. streetsi, U. plumosa, Lophothrix* sp.
81	aetideid CV
84	*Oncaea* sp.
85	*Oncaea* sp.
86	*Lophothrix* sp., *Euphausia hemigibba*, myctophid (10 mm SL)
87	*Sapphirina* sp.
93	*Nematoscelis tenella*
96	*Amallothrix* sp.
97	*Euchirella* sp., remains *Scaphocalanus* sp.
101	*Corycaeus* sp.
110	*Thysanopoda* sp. remains
111	*Gaetanus kruppi*, fish remains
188	fish remains

DISCUSSION

Vinciguerria nimbaria, V. poweriae, Valenciennellus tripunctulatus, Danaphos oculatus, and *Gonostoma atlanticum* and small *G. elongatum, G. ebelingi*, and *Diplophus taenia* were planktivorous, i.e., almost all prey were <5-10 mm long. Clarke (1978) showed that four of these species feed primarily by day, and the limited data here indicated that *Vinciguerria poweriae* does also.

The majority of the diets of *V. nimbaria* and *V. poweriae* <30 mm SL consisted of small copepods and ostracods. *Vinciguerria nimbaria* >30 mm SL appeared to feed mostly on substantially larger prey—amphipods and small euphausiids, but large calanoid copepods were not important at any size. In the western Pacific, *V. nimbaria*, apparently smaller than the smallest size group covered here, were also reported to feed mostly on small copepods and ostracods (Ozawa et al. 1977).

Certain prey types found in stomachs of *V. nimbaria*, e.g., *Scolecithrix danae, Paracandacia* spp., *Oncaea venusta, Stylocheiron* spp., were either absent or very rare in the daytime plankton samples, but most were present at moderately high densities within the nighttime depth range of *V. nimbaria* (Clarke 1980). Based on diel changes in state of digestion of prey, Ozawa et al. (1977) concluded that *V. nimbaria* fed at sunset and at sunrise; their evidence for feeding at sunrise is indirect and equivocal. Clarke's (1978) data do not preclude feeding during the upward migration at sunset, but give no indication of feeding at night or sunrise. Thus, while some of the prey types not present in the plankton by day may have been taken at sunset, it seems unlikely that any would remain intact until late

afternoon (when two of the day trawls were made) the next day. *Vinciguerria nimbaria* could conceivably undertake short, irregular excursions to shallower water during the day, or alternatively, may have a strong preference for rare, but perhaps vulnerable "stragglers" from populations with shallower centers of abundance.

For several prey types, most of the items recorded were found together in one or a few of the fish examined. This indicates that *V. nimbaria* often feeds on patches or aggregations of certain prey types. My earlier observation (Clarke 1978) that *V. nimbaria* stomachs tend to be either quite full or nearly empty throughout the day is also indicative of encounters with patches of prey. Since patchiness would increase the variability of encounter rates by both individual fish and the plankton nets, this might explain why some prey types were poorly represented by the few plankton samples as well as the large apparent differences in diet between small samples of fish.

Wherever and however *V. nimbaria* feeds, it clearly showed preference for certain prey types. Some types which were abundant in the zooplankton samples, e.g., *Oncaea* spp., *Clausocalanus* spp., small ostracods, were eaten frequently by fish <30 mm SL; but many other types, e.g., *Eucalanus* spp., scolecithricids (except *Scolecithrix danae*), *Metridia* spp., large *Pleuromamma* spp., and chaetognaths, also abundant were either absent or poorly represented in the diet. The types poorly represented in the diet were mostly either larger, less pigmented, or more translucent than those frequently eaten, regardless of whether the latter were rare or abundant in the plankton. The diet and apparent preferences of small *V. nimbaria* are most similar to but not identical with myctophids such as *Benthosema suborbitale* and *Bolinichthys longipes* which feed on small zooplankton (Clarke 1980). *Vinciguerria nimbaria* >30 mm SL showed apparent preference for *Stylocheiron* spp. and amphipods, both of which were rather uncommon within the day depth range. In contrast to both the remaining planktivorous stomiatoids and several myctophids which also feed on large zooplankton (see below), *V. nimbaria* ignored the large calanoids which were fairly abundant at the deeper end of its depth range (Table 2).

The diets of the remaining planktivorous stomiatoids were nearly restricted to large calanoids and small euphausiids. The copepods eaten were fairly abundant within the day depth ranges of the fishes (Table 2), but were apparently preferred over similar-sized *Eucalanus* spp., augaptilids, and chaetognaths which were also fairly abundant. The latter types are very translucent compared with the types eaten and probably less detectable visually. The *Gonostoma* spp. and *D. taenia* have relatively smaller eyes than *V. nimbaria* (data given in Grey 1964). Thus, the apparent preferences of these gonostomatids may result from their being poorly equipped to detect small, translucent, or otherwise less visible prey. (The sternoptychid species both have relatively large eyes, but they are tubular and directed upward, and are difficult to compare with the others.)

The diets of the planktivorous stomiatoids except *Vinciguerria* spp. were not only similar to each other but to those of three common myctophids (*Lampanyctus nobilis*, *L. steinbecki*, and *Triphoturus nigrescens*), which also have relatively small eyes (Clarke 1980). Limited data on diet from Clarke (1978) indicates that the abundant myctophids of the *Lampanyctus niger* species group also feed similarly. Thus, although they feed at different depths and times, several coexisting species of fishes are utilizing the same resources and apparently feeding selectively for the same reasons; conversely, a relatively few species of large zooplankton—particularly *P. xiphias* and *Euphausia* spp.—are supporting a large fraction of the planktivorous fishes. Certain small zooplankton, e.g., *Oncaea* spp. and *P. gracilis*, also appear to be heavily grazed by *Vinciguerria* and several other fishes from the same area (Clarke 1980), but overall there is less interspecific overlap in diet and more evidence of different feeding mechanisms among species which eat small zooplankton.

Gonostoma elongatum, *G. ebelingi*, and *D. taenia* appear to be essentially planktivores that consume some large prey simply because they reach larger sizes than do the other planktivorous stomiatoids. All three have well-developed gill rakers, none have large fangs, and the cardiac portions of the stomach are not notably elongate. Similarly, to the small individuals, the large specimens usually contained several relatively small prey; relative size of most items was ca. 10% of SL with few over 20%. Most of the prey were crustaceans, euphausiids and sergistid shrimps, but some fish and squid were taken. The only evidence of selectivity was the repeated occurrence of the relatively uncommon amphipod, *Vibilia* spp., in *D. taenia*.

The remaining species—of six families—all appear basically adapted for capture and ingestion of relatively large prey. All have large fangs, none have well-developed gill rakers, and in most the cardiac portion of the stomach is elongate and, in some species, obviously capable of distension to accommodate prey over one-half the predator's body length. All these species except *Malacosteus danae* have eaten relatively large prey (usually at least 20% of SL) at all sizes and most of them exclusively such items. There was rarely more than one prey item in a stomach.

Juvenile *Thysanactis dentex* and *Astronesthes* spp.—especially *A. indicus*—were the only fishes of this group that routinely ate zooplankton. Those consumed by small *A. indicus* were ostracods and small copepods, generally similar to the diet of *Vinciguerria nimbaria*. The juvenile *T. dentex*, which were larger than the planktivorous stages of *A. indicus*, had eaten mostly large calanoids and small euphausiids, essentially the same eaten by similar-sized *Gonostoma* spp. In both species, however, the incidence of relatively large prey was as high in the small planktivorous stages as in the sizes which ate only large prey. Thus, rather than changing with growth from small to large prey (but of the same range of relative size), these species appear to prey on an increasingly narrower range of relative sizes of prey.

Most of the nekton-eating stomiatoids were principally or exclusively piscivorous. The *Photostomias* spp. were the only ones that never ate fish. The relatively large prey of juvenile *A. indicus* and *A. "cyaneus"* were euphausiids, but there was limited evidence that adults of both species are piscivorous. The smallest size group of *Chauliodus sloani* and all sizes of *T. dentex* had eaten some relatively large euphausiids or sergestids; usually these were relatively smaller than the fishes eaten. Otherwise, crustaceans were either a minor or suspect part of the diet.

The systematic examinations of fairly large numbers of specimens by Beebe and Crane (1939), Legand and Rivaton (1969), and Borodulina (1972), and many other isolated reports in the literature generally agree that species of the six families considered as nekton-eating here eat primarily or exclusively relatively large prey which are usually fish. The only well-documented exception is *Tactostoma macropus*, which appears to eat only euphausiids and sergestids (Borodulina 1972). Notes by Fitch and Lavenberg (1968) indicate that off California several congeners of piscivorous Hawaiian species routinely eat crustaceans and that one, *Bathophilus flemingi*, eats "small crustaceans almost exclusively." The discrepancies may be artifacts due to differences in towing speed (not given by Fitch and Lavenberg and most other studies). The same types of differences were observed between specimens from the same area collected at speeds of over or under ca. 1.5 m/s (see Methods).

There was evidence of selectivity by the predators among the potential prey fishes. All but one of the fishes identified from stomachs were vertically migrating species; in particular, the nonmigrating *Cyclothone* and *Sternoptyx*, which are abundant within the day depth ranges of the predators, were absent from the diets of all predators except *Heterophotus ophistoma*. Other stomiatoids, particularly the abundant *Vinciguerria* spp., were underrepresented, and the abundant myctophids of the *L. niger* complex were absent. Based on the relative abundances of different migrating fishes in the study area (Table 9), several species of predators took cer-

TABLE 9.—Relative abundance and estimated average biomass (wet weight) of vertically migrating fishes based on data from 58 oblique trawls taken at night near Oahu, Hawaii, in 1977-78. Total number of fishes caught was 14,084. Relative abundance is expressed as percent of total myctophids, the dominant group.

Species	Relative abundance as % of total myctophids		Average biomass ($gm/10^3/m^2$)
	Numbers	Biomass	
Stomiatoids:			
Small planktivores		1.2	5.4
Vinciguerria spp.	13.0		
Others	2.8		
Gonostoma spp., *Diplophus taenia*	7.6	18.1	80.8
Nekton-eating species		15.9	66.4
Astronesthes spp.	0.7		
Chauliodus sloani	0.4		
Idiacanthus fasciola ♀	1.2		
Thysanactis dentex	0.9		
Eustomias spp.	0.8		
Photostomias spp.	0.6		
Others	0.6		
Myctophids:		100	455.5
Lampanyctus "niger" complex	13.0		
Lampanyctus spp. (others)	25.6		
Ceratoscopelus warmingi	14.2		
Diaphus spp.	12.6		
Notolychnus valdiviae	12.0		
Triphoturus nigrescens	5.1		
Benthosema suborbitale	5.1		
Bolinichthys longipes	3.4		
Others	8.9		
Other planktivores:		6.2	27.6
Melamphaeidae	3.7		
Bregmaceros spp.	1.8		
Cheilodipteridae, Notosudidae, etc.	0.9		
Other nekton-eating species:		4.5	20.2
Eels	0.5		
Iniomi, Trichiuroids, Chiasmodontidae, etc.	1.3		

tain prey species much more frequently than would be predicted by random nonselective feeding. Examples include nonmyctophids, particularly *Bregmaceros* spp., in the diet of *Thysanactis dentex*; *Bolinichthys longipes* in *Eustomias bifilis*; *Howella* spp. in *E. enbarbatus*; *Diaphus* spp., *Howella* spp., and *Scopelosaurus* spp. in the *Eustomias* spp. with two pectoral rays; and *Notolychnus valdiviae* in *Leptostomias* spp. The probability of drawing at random, e.g., two *Howella* spp. or two *Scopelosaurus* spp. out of two fish from the fauna is very low.

The relative sizes of fish prey for most species of predators were 20-30% of SL. Many of the values over 30% were for relatively slender prey such as *Bregmaceros* or *Scopelosaurus*. Only the *Bathophilus* and *Photonectes* spp. and small *Chauliodus sloani* appeared to take prey >30% routinely. The values for *I. fasciola* were mostly <20%; this species is, however, so slender that the relative size in terms of head length or body weight would be more like those for the other species.

If the weights of predator and prey were both similarly related to the cube of the length, then 20-30% relative length gives a value of 0.8-2.7% of body weight per item. If anything, this is probably an underestimate of average prey size, since the predators are for the most part slenderer than their prey. Also the stomiatoids seem to be softer bodied than most of their prey and may have a higher water content (cf. Blaxter et al. 1971); this would mean that relative prey size in terms of dry weight is higher. Borodulina (1972) gives lengths (SL ?) and wet weights of 14 fish prey and stomiatoid predators. The relative lengths of prey were 12-52% and relative weights 0.1-2.8%. The latter are probably underestimates of relative weight since some losses of prey weight must have occurred even in specimens still intact enough to be measured.

With the exceptions of *A. indicus* and *T. dentex*, all species with chin barbels fed exclusively or nearly so on relatively large fish. The barbel is rudimentary in *C. sloani*, which was also piscivorous except at the smallest sizes, but *C. sloani* has an elongated first dorsal ray with a light organ on the tip. Of the other nekton-eating species without barbels, fish were absent from the diets of the *Photostomias* spp. and eaten only by the largest *M. niger* and *A. "cyaneus."* The large gonostomatids also lack a barbel. Fish were less frequent than large crustaceans in their diets and were relatively smaller than fishes eaten by the predators with barbels. *Tactostoma macropus*, the only melanostomiatid known to eat primarily crustaceans (Borodulina 1972), has the smallest and most rudimentary barbel in the family.

Although there are no directly supportive data or citations, it is undoubtedly true that in the open ocean, crustaceans far outnumber fishes at lengths <15-20 mm; for lengths >25-35 mm the opposite is probably true. It is also probably true that a fully metamorphosed fish is a faster swimmer than a similar-sized crustacean and, other things being equal, more likely to evade capture when attacked by a predator. Thus a predator which preferred items 20-30% of its length and actively searched for prey would have a diet similar to those of *A. indicus* and *A. "cyaneus."* The small predators would encounter crustaceans much more frequently and probably capture those encountered more frequently than they would fish, while the large predators would almost be forced into piscivory due to the relative rarity of appropriate-sized crustaceans. If the predator preferred prey only 10% of its body length, the diet would resemble those of the large *Gonostoma* spp., where even the largest individuals (100-200 mm) would still encounter more crustaceans than fish in the appropriate size range.

Most of the fishes with barbels must either reject crustaceans encountered or feed other than by active search. A plausible and likely hypothesis (which has been suggested by others) is that they are "passive" and use the luminescent bodies in the barbel to attract prey. Bertelsen (1951) developed a similar hypothesis for the ceratioid angler fishes. Since several of the prey fishes are not known to be bioluminescent themselves, it is most probable that the barbel mimics food of the prey species—most of which appear to be primarily visual feeders (see above)—rather than a conspecific of the prey. The large crustaceans apparently are not similarly attracted; this is not surprising in view of their very different eyes and probably different diet and feeding behavior. Thus the barbel may be an adaptation for attracting and perhaps aiding in capture of relatively large fish. This mechanism could allow these stomiatoids to subsist on relatively large prey whose densities are quite low (on the order of $1/m^2$ of sea surface, see Maynard et al. 1975) with less energy expenditure than would be required for active search and capture. Furthermore, assuming the findings of Pandian (1967)

are generally true, the fish, which appear to be preferentially attracted, would be more efficiently digested and converted than crustaceans.

Chin barbels (and the first dorsal ray of *Chauliodus*) are not fully developed until after metamorphosis; for most species covered here, the smallest specimens examined (Tables 6, 7) are roughly the size at which the barbel appears fully developed. The *Astronesthes* spp. are quite small at metamorphosis, and it is not surprising that they apparently eat some of the zooplankton encountered regardless of whether or not they possess a barbel. Likewise, newly metamorphosed *C. sloani* would be expected to encounter so many more appropriate-sized crustaceans than fish that it would include some of the former in its diet. Bertelsen (1951) has similarly suggested that juvenile ceratioids eat some items as a result of visual detection and capture rather than by use of their lures. (The *Bathophilus* and *Photonectes* spp. are almost as small at metamorphosis as *C. sloani*, but, perhaps because they can handle relatively larger prey, appear to feed in the passive mode immediately after acquiring a barbel.) *Astronesthes indicus*, however, continues to feed like the barbelless *A. "cyaneus,"* i.e., as would be predicted for an actively searching species, until at least up to ca. 60 mm. *Astronesthes indicus* is unique in that the barbel is not fully developed shortly after metamorphosis but changes considerably as the fish approaches adult size (Gibbs 1964); consequently, it may not begin to feed passively until later.

Thysanactis dentex has a well-developed barbel, metamorphoses at rather large size, and appears to capture fish as frequently as the other species with barbels; but it also feeds on zooplankton until it is fairly large and includes relatively large crustaceans in its diet at all sizes. It thus appears to feed as an actively searching visual predator as well as by using the barbel. In spite of the advantages suggested for passive feeding, *T. dentex* is obviously successful at combining both methods; except for *Idiacanthus fasciola*, it is by far the most common species of the barbelled stomiatoids in the study area (Table 9).

Assuming that the above hypotheses are valid, then evidence for selective feeding by some species indicates that interspecific differences in barbel morphology and, perhaps, methods of deployment have evolved to specialize in attraction of a restricted type of prey, i.e., some of the species may be analogous to devoted aficionados of fly fishing in *Homo sapiens*. Although even the "generalist" *T. dentex* showed some evidence of preference for certain fishes, most evidence of restricted diets was from *Eustomias*, which is the most speciose genus considered and also has the most varied and ornate barbels. If sufficient data become available, it would be pertinent to compare the degree of preference in *Eustomias* with, e.g., *Bathophilus* or *Aristostomias*, in which all the species have similar and rather plain barbels. Regardless of whether the barbel is used or not, the advantages of specialization in diet, such as increased efficiency of capture, must be great. The overall density of prey in the study area is low compared with other oceanic areas, and much current ecological theory (e.g., Schoener 1971; Werner and Hall 1974) would predict broad diets rather than restriction to a single prey type such as *Scopelosaurus* spp., whose density is $<1\%$ of the already low total fish density.

The *Photostomias* spp. have no obvious features that would predict a diet restricted almost totally to sergestids. Though they lack a barbel, this would not explain the total absence of fish from the diet. The absence of caridean shrimps from their diet, as well as from those of the other species, may be related to stouter exoskeleton and heavier spines in these shrimps than in sergestids, but there are no such features to suggest why the very abundant large euphausiids and penaeid shrimps are also nearly completely ignored. *Photostomias* must either be able to attack and detect only sergestids or have some method of luring only them into proximity.

Malacosteus niger is the only "nekton-eating" predator which does not vertically migrate (Clarke 1974). Zooplankton densities within most of its depth range are low both day and night, but by day it overlaps with several abundant vertically migrating fishes as well as sergestids (Walters 1977) and large euphausiids (Hu 1978). Since this species is apparently well adapted for ingestion of large prey, has one of the largest gapes of all stomiatoids (Morrow 1964), and is so poorly adapted for small prey—no gill rakers or floor to the mouth, it is all the more perplexing that it had eaten so few relatively large items. It appears to subsist on a rather odd assortment of copepods.

Among the nekton-eating species, there were few differences between day- and night-caught fish in the incidence of intact prey, and none of the differences were sufficiently large to allow any inference about feeding chronology. There

is some indirect evidence for night feeding. Most of the predators are found with their prey both day and night; however, some prey, the *Bregmaceros* and *Melamphaes* spp., occur well below their predators during the day (Clarke and Wagner 1976) and could only have been eaten at night or during migration. The absence of nonmigrating species in the diets also indicates less or no feeding during the day. Finally, if the lures of these predators are used to attract fish which are themselves actively searching for prey, the high frequency of species which feed in the upper layers at night and the low frequency of day-feeding, but vertically migrating, stomiatoids also indicates night feeding by the predators.

The average biomass of the nekton-eating stomiatoids in the study area was a substantial fraction of that of their prey (Table 9) and indicates that they are probably an important source of mortality to the prey species. An estimate of the stomiatoids' impact on the prey populations can be made from the catch and stomach content data from the 1977-78 series of oblique trawl tows and estimates of stomach evacuation time. The entire series of tows caught 17,543 vertically migrating planktivorous fish of the types eaten by the stomiatoids: Myctophids, exclusive of the *Lampanyctus niger* complex, plus other non-stomiatoid planktivores. The same tows caught 822 nekton-eating stomiatoids, exclusive of *Photostomias* spp. A minimum of 111 fishes or fish remains were found in the stomachs of these predators. If the totals from this extensive series of samples are taken as representative of the average state in the study area, then on the average the nekton-eating stomiatoids consume 0.63% of the prey numbers over a period of time equal to that required to evacuate the stomach.

This estimate is likely to be low because both feeding incidence of the predators and their numbers relative to the prey are probably underestimated. There were 107 stomiatoids whose stomachs were ruptured, and any prey they might have contained are not included. In fact, it is possible that individuals with distended stomachs were more susceptible to damage during capture and consequently, that the incidence of prey in the damaged specimens might have been higher than in the undamaged ones. The numbers of both predators and prey caught by the trawls are both negatively biased due to avoidance of the net, but there is evidence that the larger stomiatoids, especially *Astronesthes* spp., are much better avoiders than the small planktivores (Clarke 1973, 1974). Unless there was a difference in bias between stomiatoids with full and empty stomachs, this would also result in an underestimate of the percent of the prey population consumed.

There are no available data to directly estimate the time required to evacuate the stomach for these fishes, but studies of other fishes fed comparable sized meals indicate that evacuation time is no longer than 4 d and probably less. Evacuation times determined at temperatures similar to those encountered by the stomiatoids at night (15°-25°C) are mostly less than a day (Pandian 1967; several studies summarized by Magnuson 1969); at temperatures similar to those of the day depths (4°-5°C) values are 2-4 d (Tyler 1970; Popova and Sytina 1977). If evacuation time were 4 d, the annual consumption by stomiatoids would be 57.5% of the average standing crop of prey (0.63% $\times$ 365/4); if the time were 1 d, consumption would be 2.3 times the standing crop.

Although annual production by vertically migrating planktivorous fishes probably exceeds the average standing crop (Clarke 1973), the estimated consumption by piscivorous stomiatoids indicates that the latter account for a large and possibly predominant share of the former's production. Though stomiatoids appear to be the most abundant piscivores, consumption of the migrators by other, similar-sized predators, e.g., scopelarchids, chiasmodontids, trichiuroids, eels, and squids, is also likely to be substantial. The migrating planktivorous fishes, in turn, appear to be the dominant group of plankton consumers in the tropical open ocean (Clarke 1973; Maynard et al. 1975). Together, these indicate that a large fraction of primary production is eventually channeled into small predators, smaller than the average planktivore in many other parts of the ocean, rather than into large, commercially harvestable species.

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I am indebted to many people who assisted in collection and sorting of the samples from which these fishes were taken and also to the crew of the RV's *Teritu*, *Moana Wave*, and *Kana Keoki*. K. Gopalakrishnan identified most of the euphausiids and decapods and capably taught me how to identify the remainder. This research was supported by NSF GA-38423, NSF OCE 77-09202, and the Hawaii Institute of Marine Biology.

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DESCRIPTION OF LARVAE OF THE GOLDEN KING CRAB, *LITHODES AEQUISPINA*, REARED IN THE LABORATORY

EVAN HAYNES[1]

ABSTRACT

Larvae of golden king crab, *Lithodes aequispina*, were reared in the laboratory from Stage I through Stage V (glaucothoe). Each of the five larval stages is described and illustrated. Zoeae of *L. aequispina* are distinguished from zoeae of *L. maja* and *L. antarctica* by the number of telsonic setae and the length of the posterolateral spines on somites 2-5. The glaucothoe of *L. aequispina* are distinguished from glaucothoe of *L. maja* and *L. antarctica* by the terminal configuration of the carapace spines. Zoeae of *L. aequispina* are distinguished from zoeae of *Paralithodes* spp. by number of telsonic setae and by setation of the antennal flagellum. Morphological differences between larvae of Lithodidae and Paguridae are greater than previously believed.

Information on the larval stages of the genus *Lithodes* is meager—only the larvae of *Lithodes maja* (Linnaeus) from the North Atlantic Ocean and larvae of *L. antarctica* (Jacquinot) from the South Pacific Ocean have been described (Sars 1890; MacDonald et al. 1957; Campodonico 1971). In this paper, I describe larvae of the golden king crab, *L. aequispina* (Benedict), from the North Pacific Ocean and compare them with larvae of *L. maja*, *L. antarctica*, and *Paralithodes* spp., and with larvae of the subfamily Pagurinae (family Paguridae).

METHODS

An ovigerous *L. aequispina* releasing larvae was collected from waters of southeastern Alaska (lat. 58°41.5'N, long. 135°05'W) during a National Marine Fisheries Service trawling survey. The specimen was caught 9 March 1979 at 292 m. Bottom water temperature was 2.3°C. The female was placed in about 2,500 l of filtered seawater at 2.3°C. Hatching resumed immediately, and the first samples were taken about 10 min later. No prezoeae were seen. The samples were preserved in a 5% solution of Formalin[2] and seawater.

About 4 h after hatching, 10 larvae were transferred to each of 30 250 ml jars containing about 200 ml of filtered seawater at 6.8°C. The jars were checked daily for exuviae, and a few larvae were preserved every other day. The individuals and cast skins of various stages provided a continuous sequence of stages. Seawater in the holding containers was changed every other day, and the larvae were fed plankton daily that was strained through a 0.333 mm mesh. The density of food was controlled only to the extent that a few food items remained in the container at the end of each feeding period.

Terminology, methods of measuring, techniques of illustration, and nomenclature of appendages follow Haynes (1973, 1976). Setation formulae are the number of setae per segment from the distal segment to the proximal segment. For clarity in the illustrations, setules on setae are usually omitted, but spinulose setae are shown. A minimum of five larvae of each stage was used to verify segmentation and setation.

Only those morphological characteristics useful for readily identifying each stage are given.

STAGE I ZOEA

Mean total length of Stage I zoeae (Fig. 1A), 7.3 mm (range 6.8-7.7 mm, 20 specimens). No chromatophores; internal thoracic area orange—coloration same throughout all larval stages. Rostrum slightly sinuate, without teeth, about three-fourths length of carapace. Posterolateral spines on carapace. Eyes sessile.

Antennule (Fig. 1B).—First antenna, or antennule, with unsegmented, tubular basal portion (peduncle) and two distal, conical projections.

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

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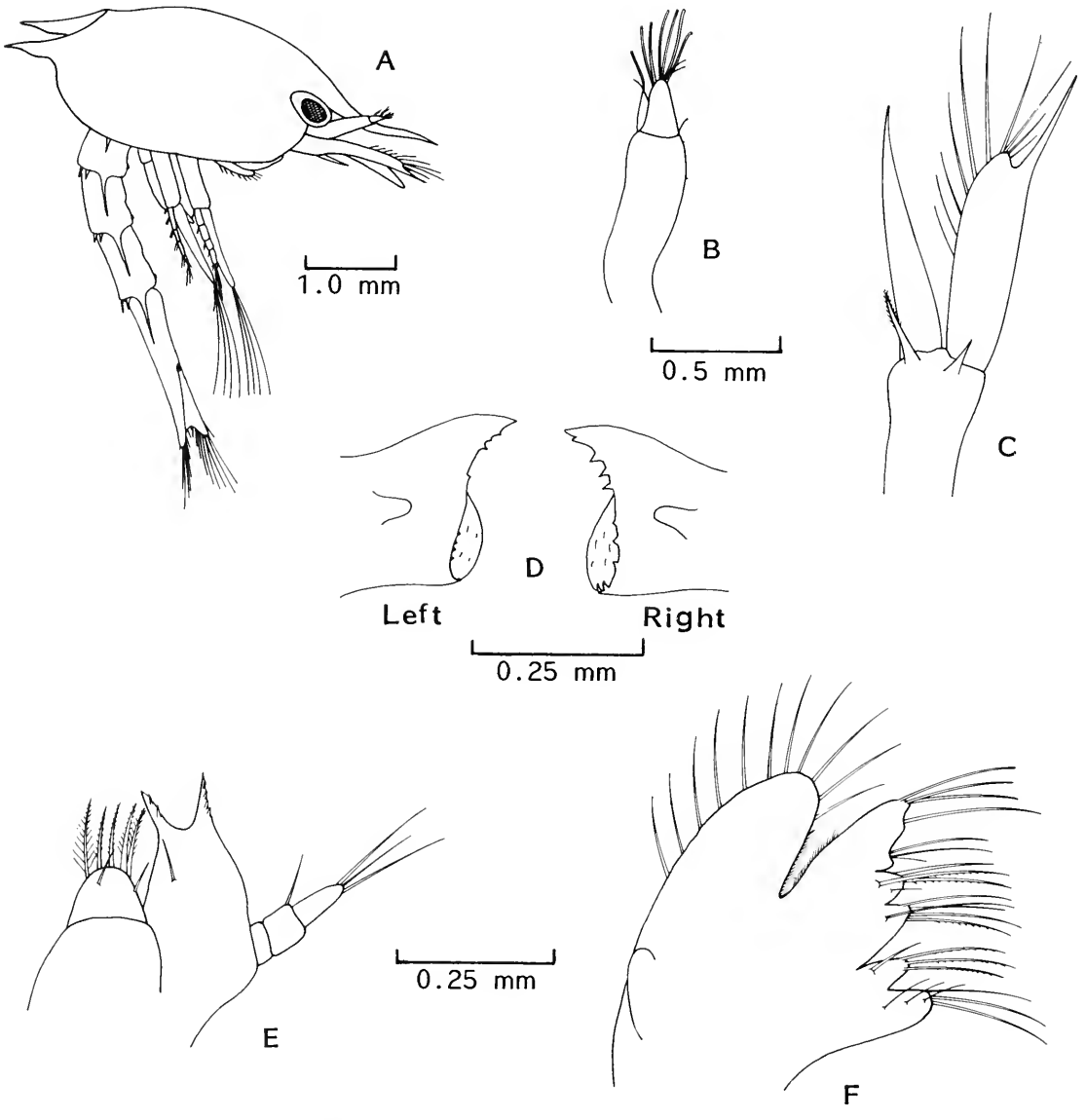
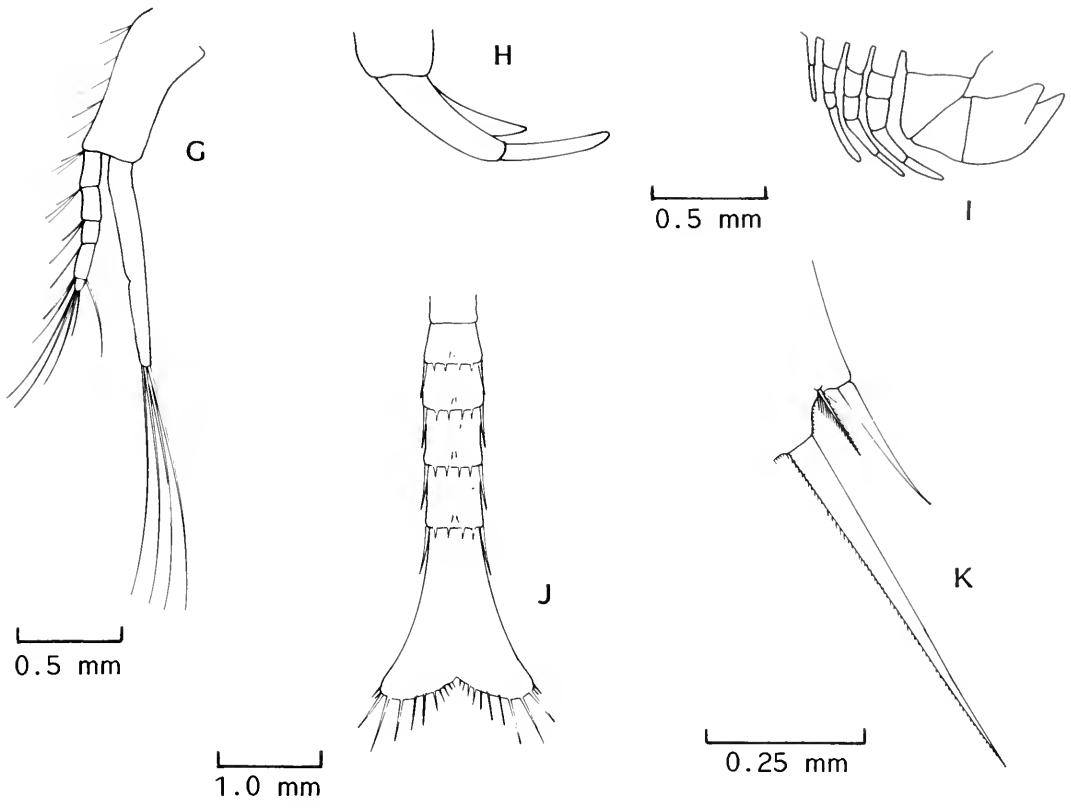


FIGURE 1.—Stage I zoea of *Lithodes aequispina*: A, whole animal, right side; B, antennule, dorsal; C, antenna, ventral; D, mandibles (left and right); E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, lateral; H, third maxilliped, lateral; I, pereopods 1-5,

Peduncle with simple seta terminally. Larger projection with two aesthetascs subterminally, four aesthetascs and two simple setae terminally. Smaller projection with aesthetasc and simple seta terminally.

Antenna (Fig. 1C).—Second antenna (antenna) with inner flagellum (endopodite) and outer antennal scale (exopodite). Naked flagellum unsegmented, slightly shorter than scale (scale length includes spine). Antennal scale unjointed distally, fringed with 10 heavily plumose setae along terminal and inner margins; prominent spine distally on outer margin. Ventral surface of protopodite with spinulose spine at base of flagellum, naked spine at base of scale. Shape and spination of protopodite same as in later zoeal stages except fewer spinules on spinulose spine.

Mandibles (Fig. 1D).—With unsegmented palps in all larval stages. Incisor process of left man-



lateral; J, abdomen and telson, dorsal; K, minute seta of telson, ventral.

dible a tooth; right mandible with diserrate incisor process. Anterior margins of each mandible with three or four small teeth between incisor and molar processes. Neither mandible with subterminal tooth on molar process in any larval stage.

Maxillule (Fig. IE).—First maxilla (maxillule) with coxal endites, basial endites, and endopodite. Coxopodite (proximal lobe) two-segmented, distal segment with plumose seta and six spines: four spines spinulose, two simple. Basipodite (median lobe) with two spinulose spines terminally, simple seta subterminally. Endopodite originates from lateral margin of basipodite. Endopodite three-segmented with three setae terminally and one seta distally on second segment.

Maxilla (Fig. 1F).—Second maxilla (maxilla) with platelike exopodite (scaphognathite). Exopodite with 11 long, evenly spaced plumose setae along outer margin. Future location of proximal expansion indicated by small lobe. Endopodites unsegmented in all larval stages; in Stage I, setation formula of endopodite 3, 1, 3. Basipodite and coxopodite bilobed. Basipodite with four setae on distal lobe, five setae on proximal lobe; coxopodite with four setae on distal lobe, six setae on proximal lobe.

First maxilliped (Fig. 1G).—Most heavily setose of natatory appendages. Unsegmented protopodite with 10 setae. Endopodite distinctly five-segmented; setation formula 4, 3, 1, 2, 3. Exopodite a partially segmented long, slender ramus with four terminal natatory setae.

Second maxilliped.—Essentially same as first maxilliped except endopodite four-segmented.

Third maxilliped (Fig. 1H).—Endopodite and exopodite undeveloped, naked; exopodite two-segmented.

Pereopods (Fig. 1I).—Poorly developed, without exopodites in all larval stages; segmentation may be indistinct.

Pleopods (Fig. 1A).—Absent on first somite in all larval stages; in Stage I, present on somites 2-5 as distinct buds. Pleopod 6 absent until Stage III.

Abdomen and telson (Fig. 1A, J).—Abdomen with five somites and telson (somite 6 fused with telson until Stage IV). Somites 2-5 with pair of posterolateral spines, four short spines along posterior margin, pair of hairs near dorsoposterior margin. Telson slightly emarginate posteriorly, with 11 + 11 (rarely 10 + 11) densely plumose setae. Ninth pair of setae on telson longest, almost one-third telson width. All setae jointed with the telson except ninth pair; ninth pair fused with telson. Minute plumose seta between setal pairs 10 and 11 (Fig. 1K). Except outer pair of setae, setae with setules. Setules along terminal margin between bases of setae. Without uropods in all larval stages. Anal spine absent in all larval stages.

STAGE II ZOEA

Mean total length of Stage II zoeae, 7.5 mm (range 7.0-8.0 mm, 10 specimens). Rostrum and carapace same shape as in Stage I. Eyes stalked.

Antennule (Fig. 2A).—Large plumose seta and three small simple setae at distal joint of unsegmented peduncle.

Antenna (Fig. 2B).—Two-segmented flagellum extends slightly beyond plumose setae of scale. Antennal scale with 9 (rarely 10) heavily plumose setae along terminal and inner margins.

Mandibles.—Essentially same as in Stage I except with a few more teeth along anterior margin and palp slightly larger.

Maxillule.—Same as in Stage I except tip of basipodite somewhat more rounded.

Maxilla.—Scaphognathite (Fig. 2C) with 20 (sometimes 21) plumose setae along inner and outer margins; proximal expansion distinct, naked. Endopodite, basipodite, or coxopodite same as in Stage I except coxopodite occasionally with five setae on proximal lobe.

Maxillipeds.—Similar to Stage I maxillipeds, but exopodites of maxillipeds two-segmented; pairs 1, 2, and 3 with 9, 9, and 8 natatory setae, respectively.

Pereopods (Fig. 2D, pereopod 1).—Chelae of pereopod 1 similar to pereopod 1 of adult but without spines, setae, or teeth. Pereopods 2-5 same as in Stage I except longer and pereopod 5 four-segmented.

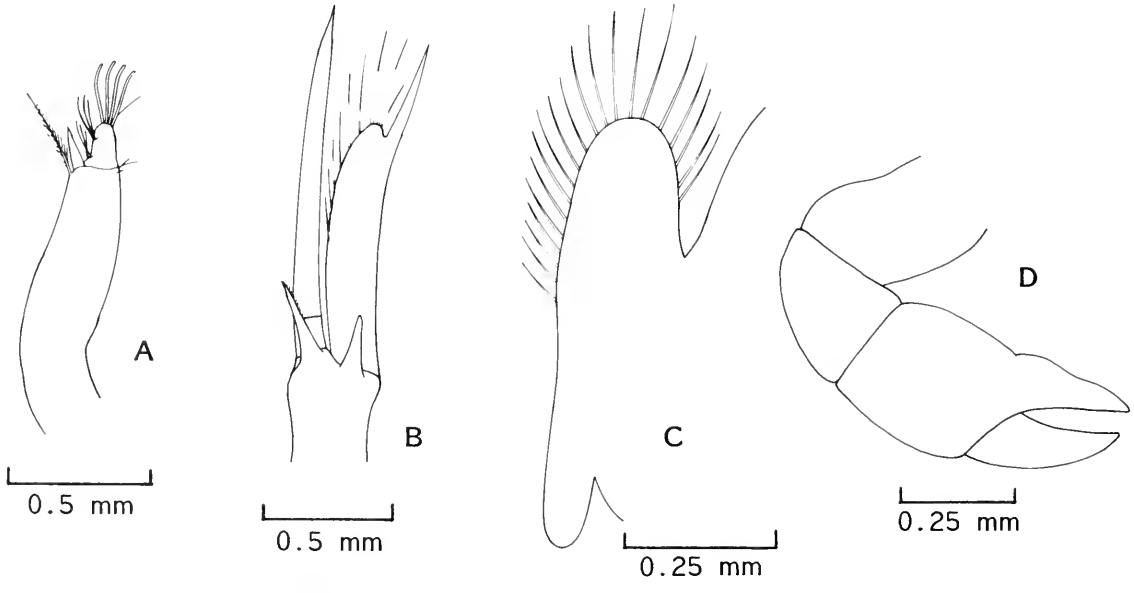


FIGURE 2.—Stage II zoea of *Lithodes aequispina*: A, antennule, dorsal; B, antenna, ventral; C, maxilla (scaphognathite), dorsal; D, pereopod 1, lateral.

Pleopods.—Pleopods 2-5 bilobed, unsegmented, without setae, about one-third height of somites.

Abdomen and telson.—Abdomen same shape and spination as in Stage I. In Stages II-IV, telson with 12 + 12 (rarely 11 + 12) densely plumose setae; tenth setal pair longest (about one-fourth telson width), fused with telson. Telson fused with somite 6.

STAGE III ZOEA

Mean total length of Stage III zoeae, 7.6 mm (range 7.4-8.4 mm, 10 specimens). Rostrum (Fig. 3A) more styliform than in Stages I and II, about one-half carapace length, with short spine and minute hair at base. Lateral margin of carapace indented just posterior to eye.

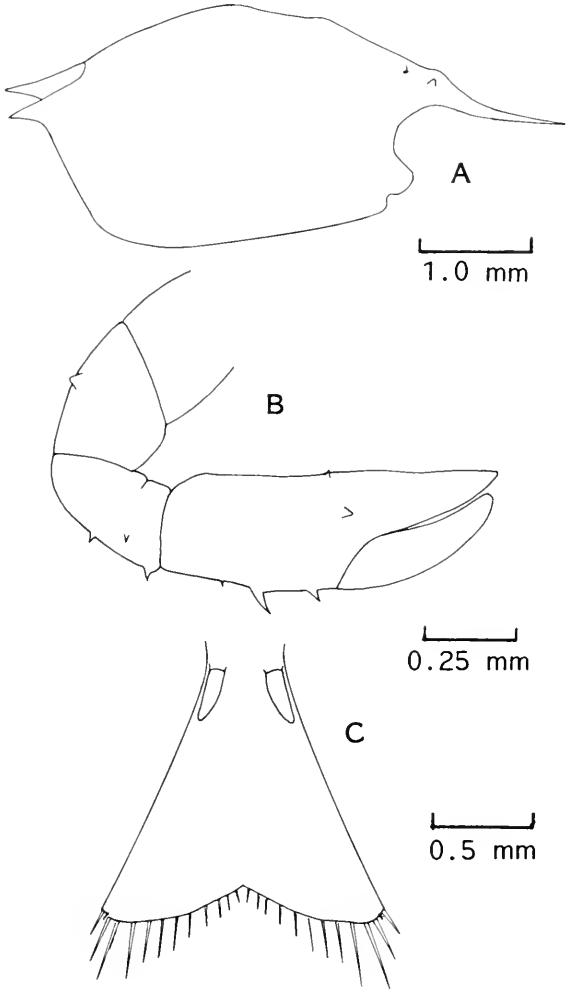


FIGURE 3.—Stage III zoea of *Lithodes aequispina*: A, carapace, lateral; B, pereopod 1, lateral; C, telson, ventral.

Antennule.—Inner projection and peduncle two-segmented; outer projection three-segmented.

Antenna.—Inner flagellum of antenna five-segmented; terminal segment with four or five simple setae and small, distinct spine at tip.

Mandibles.—Essentially same as in Stage II.

Maxillule.—Basipodite with two or three additional short, blunt spines compared with Stages I and II.

Maxilla.—Scaphognathite with 23 plumose setae along inner and outer margins; naked proximal expansion slightly longer than in Stage II.

Maxillipeds.—Essentially identical to Stage II maxillipeds except naked endopodite of third maxilliped five-segmented; exopodite with nine natatory setae.

Pereopods (Fig. 3B, pereopod 1).— Essentially identical to Stage II except chelae of pereopod 1 slightly narrower than in Stage II; protopodite usually with five spines.

Pleopods.—Lengths of pleopods 2-5 about equal to heights of somites; pleopod 6 small, nonfunctional.

Telson (Fig. 3C).—With 11 + 11 plumose setae (rarely 11 + 12).

STAGE IV ZOEA

Mean total length of Stage IV zoeae, 6.8 mm (range 6.3-7.4 mm, six specimens). Rostrum (Fig. 4A) about four-tenths carapace length. Carapace markedly more spiny than in Stage III.

Antennule.—Outer projection four-segmented, with about 14 aesthetascs; distal and penultimate segments each with long seta and two short setae.

Antenna (Fig. 4B).—Antennal flagellum eight-segmented, about 1.3 times length of scale.

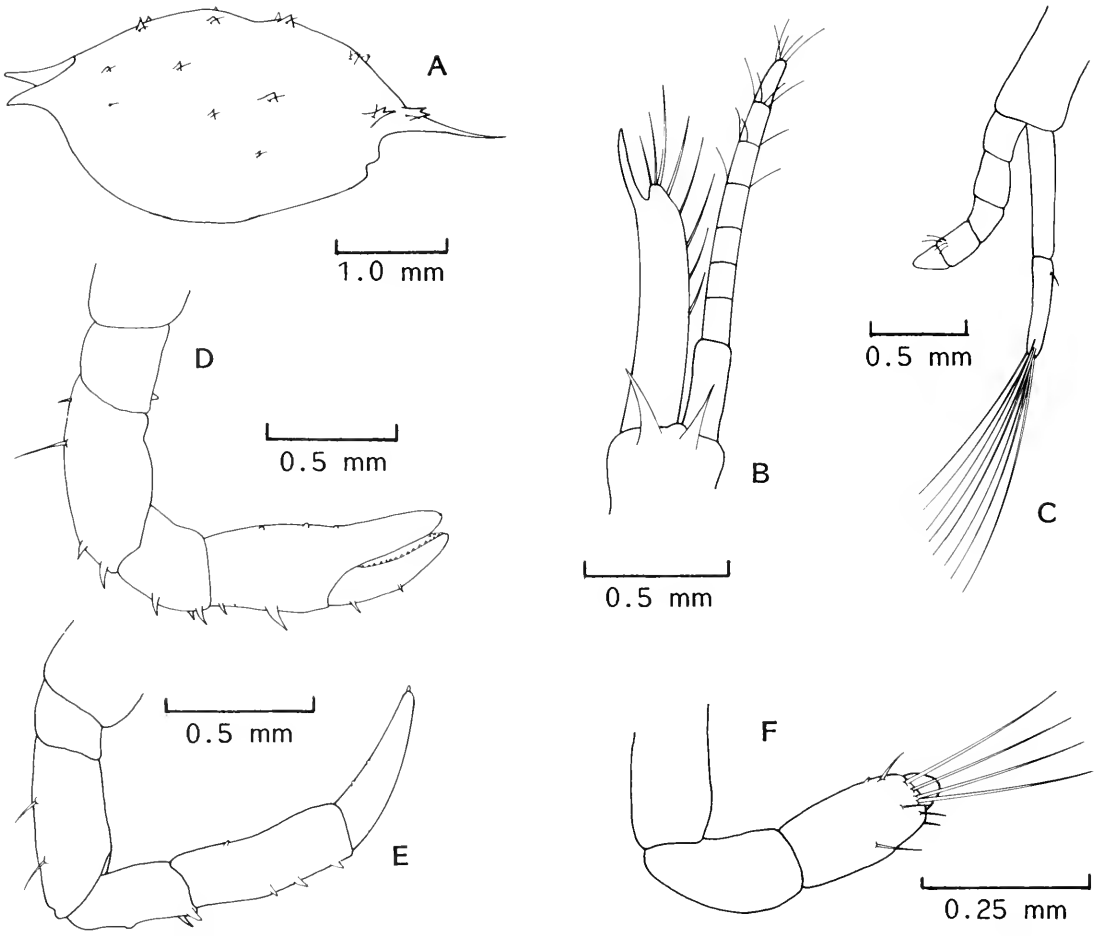


FIGURE 4.—Stage IV zoea of *Lithodes aequispina*: A, carapace, lateral; B, antenna, ventral; C, third maxilliped, lateral; D, pereopod 1, lateral; E, pereopod 2, lateral; F, pereopod 5 (terminal segments), lateral.

Terminal spine of antennal scale somewhat curved.

Maxillule and mandibles.—Essentially identical to Stage III.

Maxilla.—Scaphognathite with about 45 plumose setae along inner and outer margins.

Maxillipeds (Fig. 4C, third maxilliped).—No change in maxillipeds from Stage II except endopodite of third maxilliped with four simple setae on penultimate segment. Exopodite with eight or nine natatory setae.

Pereopods (Fig. 4D, pereopod 1; E, pereopod 2; F, pereopod 5).—Dactylopodite of chela of pereopod 1 with teeth. Pereopods 2-5 adult in shape. Propodite of pereopod 5 setose.

Pleopods.—Pleopods 2-5 about 1.4 times height of somites. Pleopods without setae; pleopod 6 unsegmented, about one-third length of telson, with two (sometimes three) short setae terminally.

Abdomen and telson.—Dorsoposterior spines on somites 2-5 reduced in size, often absent on somite 2. Telson jointed with somite 6; with 11 + 11 plumose setae (rarely 12 + 12).

STAGE V (GLAUCOTHOE)

Mean total length of Stage V larvae, 5.9 mm (range 5.2-6.3 mm, eight specimens). Glaucothoe characteristically spinous (Fig. 5A, J, K). Eye stalk with one anterior spine, three dorsal spines.

Antennule (Fig. 5B).—Adult in form.

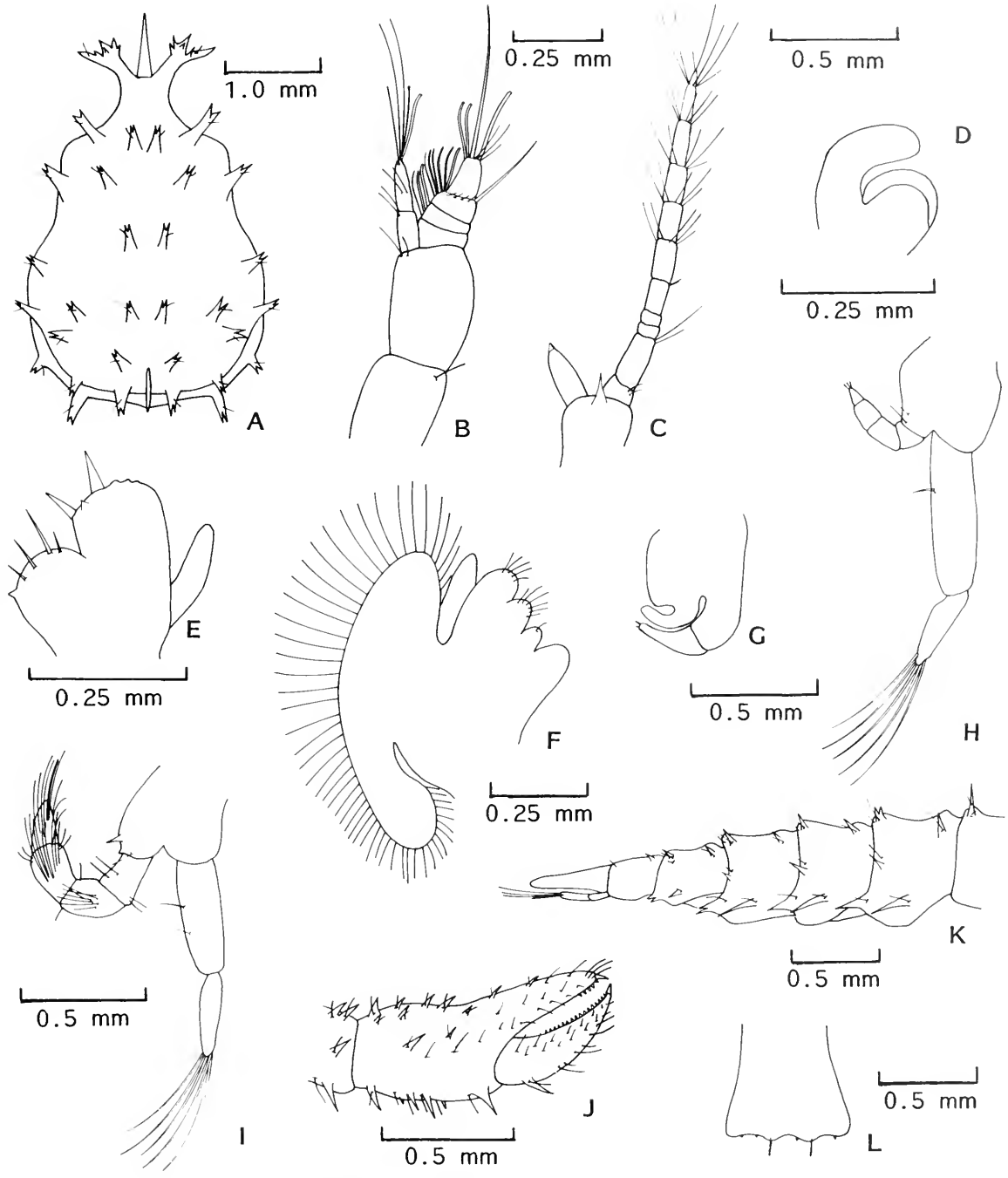


FIGURE 5.—Stage V (glaucothoe) of *Lithodes aequispina*: A, carapace, dorsal; B, antennule, dorsal; C, antenna, ventral; D, mandible (left), anterior; E, maxillule, ventral; F, maxilla, dorsal; G, first maxilliped, lateral; H, second maxilliped, lateral; I, third maxilliped, lateral; J, first maxilliped (chela), lateral; K, abdomen and telson, lateral; L, telson, dorsal.

Antenna (Fig. 5C).—Eleven-segmented flagellum more setose than in Stage IV. Scale a small projection with short spine terminally. Protopodite with spine ventrally.

Mandible (Fig. 5D).—Mandible grooved, without spines or teeth. Palp curved, naked.

Maxillule (Fig. 5E).—Coxopodite and basipodite more rounded than in zoeal stages. Coxopodite and naked endopodite unsegmented.

Maxilla (Fig. 5F).—Proximal expansion of scaphognathite somewhat bulbous. Endopodite without setae. Basipodite bilobed with five or six short setae on each lobe. Coxopodite bilobed with short seta on distal lobe.

First maxilliped (Fig. 5G).—Smaller, less developed than in zoeal stages. Endopodite and exopodite curved posteriorly; unsegmented endopodite without setae. Two-segmented exopodite with two minute spines at tip.

Second maxilliped (Fig. 5H).—Endopodite curved posteriorly, smaller and less developed than in Stage IV. Exopodite with five natatory setae.

Third maxilliped (Fig. 5I).—Posteriorly curved endopodite with numerous setae. Exopodite with five natatory setae.

Pereopods.—Chelae (Fig. 5J) of pereopod 1 typically adult, more spinous and setose than in Stage IV. Right chela slightly larger than left chela. Pereopods 2-4 typically adult in shape and spination. Pereopod 5 same as in Stage IV.

Pleopods.—Pleopods 2-5 setose, about 2.5 times height of somites. Endopodites with a few cincinnuli. Pleopod 6 with four setae terminally that extend considerably beyond telson.

Abdomen and telson (Fig. 5K, L).—Pair of dorsoposterior spines on somites 1-5. Somites 2-5 with pair of dorsoanterior spines and three pairs of posterolateral spines. Somite 6 with pair of dorsoanterior spines. All somites with hairs; one hair usually near each spine. Terminal margin of telson indented, with a few minute spines or setae.

COMPARISON OF LARVAL STAGES WITH DESCRIPTIONS BY OTHER AUTHORS

All the larval stages of *L. maja* have been described. MacDonald et al. (1957) described the two zoeal stages and the glaucothoe; Sars (1890) described the prezoea, first zoeal stage (both obtained from known parentage), and last zoeal stage (obtained from plankton). (The term "intermediate stage" in Sars' figure legend refers to the first zoea [MacDonald et al. 1957].) Sars' figures of the prezoeal telson and of Stage I are shown by Gurney (1942). The only other published description of *Lithodes* larvae known to me is that of *L. antarctica* larvae described from specimens reared in the laboratory (Campodonico 1971).

Larvae of *L. aequispina*, *L. antarctica*, and *L. maja* can be distinguished (see Table 1). In general, larvae of *L. maja* have fewer stages and are more developed for a given stage than larvae of *L. aequispina* and *L. antarctica*. In Stage I *L. maja*, the eyes are stalked, and the telson and somite 6 are jointed. In contrast, the eyes of *L. aequispina* and *L. antarctica* are not stalked until Stage II, and the telson and somite 6 are not jointed until Stage IV in *L. aequispina* and Stage

TABLE 1.—Morphological characteristics for distinguishing between larvae of *Lithodes aequispina*, *L. antarctica*, and *L. maja*. ? = no information available.

Characteristic	*L. aequispina*	*L. antarctica*	*L. maja*
No. of stages	5	4	3
Stage I:			
eyes	sessile	sessile	stalked
peduncle of antennule	unsegmented	partially segmented	3-segmented
antennal flagellum	unsegmented	partially segmented	5-segmented
telson and somite 6	not jointed	not jointed	jointed
pairs of telsonic setae[1]	11	9	8 or 9
longest pair of telsonic setae jointed with telson	no	yes	no
Stage II:			
peduncle of antennule	unsegmented	partially segmented	3-segmented
telson and somite 6	not jointed	not jointed	jointed
endopodite of third maxilliped	unsegmented	unsegmented	5-segmented
pleopods	uniramous buds	biramous	biramous
pairs of telsonic setae[1]	11	9	8 or 9
longest pair of telsonic setae jointed with telson	no	yes	no
Stage III:			
pairs of telsonic setae[1]	11	9	—
longest pair of telsonic setae jointed with telson	no	yes	—
Glaucothoe			
tips of spines on carapace	bifid	bifid	most single toothed
spine on rostral complex	6 small spines terminally	3 small spines terminally	spine bifid, no small spines terminally
natatory setae on exopodites of second and third maxillipeds	5, 5	7, 7	?

[1]In addition to a minute setal pair.

III in *L. antarctica*. The peduncle of the antennule and endopodite of the third maxilliped of Stage II *L. maja* are segmented, but are unsegmented in Stage II *L. aequispina* and *L. antarctica*.

Among genera of the family Lithodidae, larvae of *L. aequispina* are most similar morphologically to larvae of the genus *Paralithodes*. Zoeae of *L. aequispina* can be readily distinguished from *Paralithodes* zoeae (Sato 1958) by the number of telsonic setae and by the setation of the antennal flagellum. In *L. aequispina* zoeae, the telson has 11 pairs of setae in all stages, and the antennal flagellum is setose beginning in Stage III; whereas, in *Paralithodes* zoeae, the telson has nine or fewer pairs of setae, and the antennal flagellum is naked. In the glaucothoe, the carapace spines of *L. aequispina* are markedly larger and more spinous than in the glaucothoe of *Paralithodes*.

Formerly, zoeae of the family Lithodidae were considered similar morphologically to those of the subfamily Pagurinae (family Paguridae), because zoeae of Lithodidae differ only in the reduction or disappearance of the uropods (Gurney 1942; MacDonald et al. 1957). Zoeal development of *L. aequispina* and *L. antarctica* varies somewhat from the pattern of development of the other known larvae of the family Lithodidae, as summarized by Gurney and MacDonald et al. Zoeae of the Pagurinae have the following characterstics: the antennal flagellum has fewer than three setae in all stages; the telson has six pairs of setae in Stage I and seven pairs in Stages II-IV; and the exopodites of the maxillipeds have 7, 7, 6 setae in Stage II, 7 or 8 setae in Stage III, and 8 setae in Stage IV. Zoeae of *L. aequispina* have an antennal flagellum that is setose beginning in Stage III; the telson has 11 pairs of setae in all stages; and the exopodites of the maxillipeds have 9, 9, and 8 setae in Stage II and 9, 9, and 9 setae in Stages III and IV. Zoeae of *L. antarctica* differ from zoeae of the Pagurinae by having in all zoeal stages nine pairs of telsonic setae and eight setae on each exopodite of the maxillipeds. The glaucothoe of the Paguridae and Lithodidae are similar to the adults and, thus, readily distinguished from each other.

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THE SEASONAL CYCLE OF GONADAL DEVELOPMENT IN *ARCTICA ISLANDICA* FROM THE SOUTHERN NEW ENGLAND SHELF[1]

ROGER MANN[2]

ABSTRACT

The seasonal cycle of gonadal development of the ocean quahog, *Arctica islandica*, on the Southern New England Shelf was investigated by collecting adult clams at regular intervals from September 1978 to May 1980 from a 36-50 m depth transect, preparing histological sections of the gonadal tissue, and examining these microscopically for stages of development. Hydrographic measurements made concurrently with the clam collections included temperature, conductivity, dissolved oxygen, and pH. Morphologically ripe specimens were present from March through October, but predominated from May through September. A prolonged spawning period from May through November is indicated, spawning being most intense from August through November. Multiple annual spawnings at both the individual and population level were evident. After an assessment of the hydrographic conditions in the area it was hypothesized that larval survival is probably greatest during the months of October and November, which is the time of the breakdown of the intense seasonal thermocline and before the onset of low winter seawater temperatures.

Ocean quahog, *Arctica islandica* (= *Cyprina islandica*), is a large pelecypod that occurs in European waters from the White Sea to Spain (Jensen 1902; Loven 1929; Zatsepin and Filatova 1961; Punin 1978) and in American coastal waters from Newfoundland to Cape Hatteras (Nicol 1951; Merrill and Ropes 1969; Ropes 1978). The species supports an active fishery in the Middle Atlantic region and has been the subject of much recent study (Murawski and Serchuk 1979; Thompson, Jones, and Dreibelbis 1980; Thompson, Jones, and Ropes 1980; Ropes and Murawski 1980). In the Middle Atlantic region the greatest concentrations of *A. islandica* are found in depths of 25-61 m with the mean depth of occurrence increasing from 39 m off Long Island to 52 m off Virginia and North Carolina (Merrill and Ropes 1969; Ropes 1978).

The seasonal temperature structure of the waters of the Middle Atlantic region was first comprehensively described by Bigelow (1933) and has subsequently been the subject of many investigations and reviews (Walford and Wicklund 1968; Colton and Stoddard 1973; Bumpus 1973; Beardsley et al. 1976; Williams and Godshall 1977). Two important features are evident: An intense summer thermocline that builds in May and persists until September, and a "pool" of cold water (annual temperature range 2°-13°C), surrounded on both the inshore and offshore sides by warmer water, that develops on the continental shelf below the thermocline during the spring, summer, and early fall months (Ketchum and Corwin 1964; Bowman 1977). The cold pool of bottom water in the summer months overlies much of the depth range occupied by *A. islandica*. Maximum water temperatures on the sea floor in the depth range occupied by *A. islandica* occur in September and October (Bigelow 1933), and a strong relationship exists between the 16°C bottom isotherm for October and the inshore distribution limit of *A. islandica* (Bigelow 1933, figs. 49, 60; Merrill and Ropes 1969, fig. 2).

Loosanoff (1953) described the reproductive cycle of *A. islandica* based upon specimens collected regularly from commercial catches at Point Judith, R.I., from March to November (a complete annual cycle was examined but not reported). Following histological preparation and microscopic examination of the specimens, Loosanoff concluded that histological "Spawning begins near the end of June or early in July when the water temperature is approximately 13.5°C." The conclusion was based on temperature data inferred from earlier observations by Merriman and Warfel (1948). Loosanoff (1953) also concluded that spawning continued through August, and that approximately 50% of *A. islandica* examined were totally spent by early October. The larvae of *A. islandica* have been reared

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to metamorphosis by Landers (1976) and Lutz et al. (in press). Landers (1976) reported that fertilization and early cleavage were obtained at 10°, 15°, and 20°C; however, embryos only survived to the veliger stage at the two lower temperatures, and to metamorphosis at 10°-12°C. The cultures reared by Lutz et al. (in press) were maintained to metamorphosis at temperatures ranging from 9° to 13°C; but none of these investigators defined the maximum temperature at which metamorphosis could be effected.

After reviewing data on seasonal water temperature structure in the Middle Atlantic Bight and the reproductive biology of *A. islandica* reported by Loosanoff (1953) and Landers (1976), certain inconsistencies were evident. It has long been suspected that bivalve larvae can partially control their position in the water column by swimming (Carriker 1961; Wood and Hargis 1971; Cragg and Gruffydd 1975). If *A. islandica* spawn in July, then larvae swimming upwards to the regions of highest primary productivity, and hence phytoplankton food, would encounter both an intense thermocline at 20-30 m depths and surface temperatures in excess of 20°C. Both temperature conditions would be either deleterious to growth or even lethal according to Landers (1976). Therefore, it would appear appropriate to hypothesize that spawning in October or November would be more congenial to larval survival because, after the fall thermocline breakdown and subsequent vertical mixing of the water column, vertical movement of the larvae would not be limited by an intense thermocline. Furthermore, any temperature stratification that did exist at this time would have widely spaced vertical isotherms and thus form only weak barriers to horizontal dispersion.

A need was evident to simultaneously assess the reproductive cycle of the adult *A. islandica* and hydrographic conditions affecting it and larval survival. This study describes the gametogenic cycle of adult *A. islandica*, based on microscopic examination of histological preparations from individuals collected regularly from several depths over a 2-yr period, and concurrent physical data collected during the same period.

METHODS AND MATERIALS

Fourteen collections of *A. islandica* were made at intervals of 4-8 wk from September 1978 to May 1980 at depths ranging from 27 to 50 m in the vicinity of Block Island, R.I. Stations at 27-30 m depth (Station A) were north and east of Block Island (lat. 41°19′N, long. 71°34′W and lat. 41°13′N, long. 71°32′W, respectively). Stations at 36, 42, and 48-50 m (Stations B-D, respectively) were on a transect directed due south at long. 71°31′W at lat. 41°11′N, 41°03′N, and 41°01′N, respectively. Specimens were collected with a commercial hydraulic clam dredge (blade width 1.54 m, pump pressure 5.63-7.0 kg/cm^2, 7.5 cm diameter ring size; tows of 5-min duration) during the period September 1978-August 1979 and with a nonhydraulic clam dredge (blade width 0.62 m; 5.0 cm diameter ring size; tows of 20-30 min duration) during September 1979-June 1980. Both dredges were selective for clams larger than the diameter of the rings.

The clams were opened on board the vessel and either the soft tissues removed whole, or a section of tissue approximately 1 cm^2 excised from the surface of the midventral region. The tissues were preserved in Bouins fixative for 24-48 h, rinsed in water for 6 h, and stored in 70% ethanol. Histological preparation of tissue sections included embedding in paraffin, sectioning at 7 μ, staining with Delafield's hematoxylin, and counterstaining with eosin Y by the procedure of Humason (1962). A minimum of 15 specimens was examined from the midventral samples collected on each collection date. An additional five specimens of whole animals from each collection date were examined in tissue excised from each of the dorsal, midventral, and ventral regions in order to assess the uniformity of development throughout the gonadal tissue. Slide preparations were examined microscopically for evidence of gametogenesis and spawning (Holland 1972), and each was classified into one of five categories of gonadal condition, by the criteria of Holland and Chew (1974) as follows:

Early active:
- Male: Many follicles: spermatogonia and spermatocytes numerous, no spermatozoa.
- Female: Oogonia arising from stem cells along the follicle; no free oocytes. Nuclei stain darker than cytoplasm.

Late active:
- Male: Follicles contain predominantly spermatids and spermatozoa.
- Female: Both free and attached oocytes present. Ooeytes have nuclei that stain

lighter than cytoplasm and a distinct nucleolus.

Ripe:

Male: Follicles filled with spermatozoa in swirling patterns.

Female: Predominantly free oocytes with distinct nucleus and nucleolus.

Partially spent:

Male: Follicles disorganized and often empty. Some full follicles remaining.

Female: Follicles disorganized. Some mature ova remaining, some undergoing cytolysis.

Spent:

Male: Follicles disorganized and empty, few spermatozoa remaining.

Female: Follicles disorganized and empty, few ova remaining.

The report of Loosanoff (1953) was used for comparison throughout the procedure. The classification of gonadal development into stages is, by definition, qualitative. A quantitative option of describing female gonadal development as a function of mean ova diameter was considered inapplicable in the present study because ova were often elongated or otherwise nonspherical in shape, especially during development from oogonia to oocytes.

Hydrographic measurements were made at each station on each collection date. A vertical profile, from surface to bottom at 5 m intervals, was made of temperature and conductivity using either a model 6D or S8000 Hydrolab Water Quality Analyser (Hydrolab Corporation, Austin, Tex.)[3] and the conductivity measurements were converted to salinity. On six occasions these data were supplemented by vertical profiles of dissolved oxygen content and pH measured with the same instrument.

RESULTS

Hydrographic Observations

Figure 1 depicts the seasonal temperature structure of the water column at Stations A-D. No marked differences were recorded between the 2 yr of the study; hence data have been pooled. An intense seasonal thermocline was initiated in April-May and reached a maximum intensity at between 20 and 30 m depths in August. Surface waters cooled during the fall months of September and October. A uniform temperature structure throughout the water column was evident from November through April.

The intense nature of the thermocline and its relationship to depth at sample stations (A-D) is illustrated in Figure 2 for August 1979. Maximum bottom temperatures recorded at Stations A-D, respectively, were 15.4°, 14.0°, 12.9°, and 12.6°C, and they occurred earliest at the two shallower stations.

Salinity values recorded during the study agreed well with those reported previously by Ketchum and Corwin (1964). Surface to bottom salinities increased from 30.90‰ to 32.08‰ during July at Station A and from 31.59‰ to 32.85‰ at Station D. Salinities were highest but relatively stable throughout all depths and stations during the winter months (all values ranged from 32.30‰ to 33.52‰).

Dissolved oxygen data were in general agreement with those summarized for the Middle Atlantic region by Williams and Godshall (1977). Surface waters to 20 m depth were at or within 10% of saturation throughout the year. A gradual decline in percentage saturation was evident below the seasonal thermocline from April to late August (Fig. 3A). This was most obvious immediately adjacent to the sediment-water interface where a minimum dissolved oxygen level of 65% saturation was recorded at Station D in August 1979. Concurrently pH also decreased reaching a minimum of 7.9 (Fig. 3B) at the sediment-water interface at all stations in August 1979.

Gonadal Observations

Arctica islandica is dioecious. Out of 669 specimens, hermaphroditism was found in only 2 individuals which contained spatially separate developing male and female follicles (Fig. 4). Serial sectioning indicated that gonadal maturation occurred initially in tissues at the dorsal extremity of the gonadal mass and progressively later moving toward the ventral extremity (Fig. 5). Multiple spawnings in the same animal during one annual cycle, originating from tissues in a similar spatial sequence, were suggested by the presence of spent follicles in dorsal sections, while follicles in the ventral sections of the same specimen were in late active or ripe condition. No evidence was found of a second maturation of spent, dorsal gonadal follicles following spawn-

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

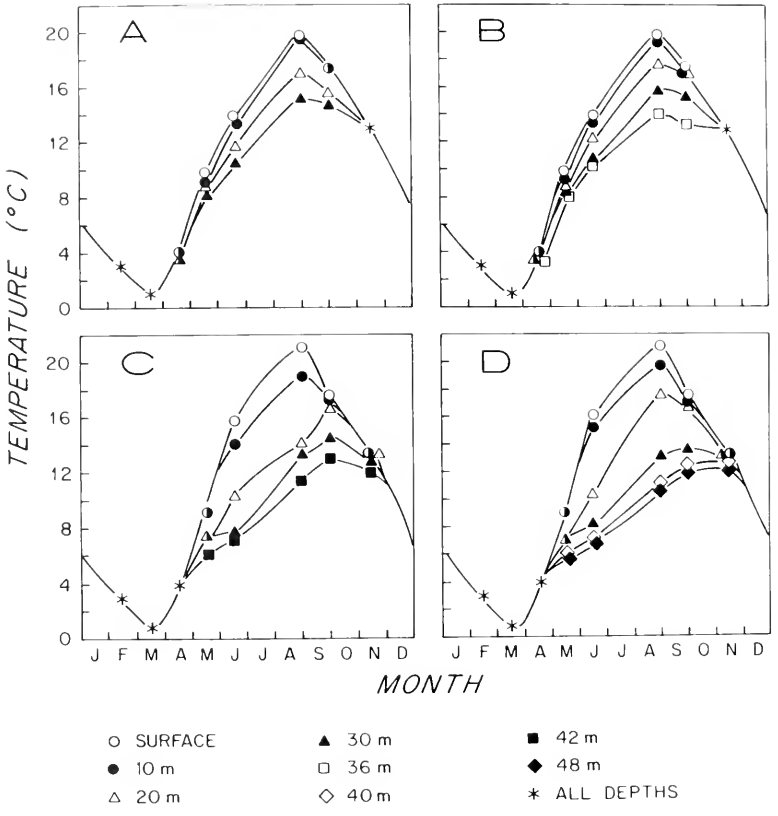

FIGURE 1.—Seasonal changes in seawater temperature at 10 m intervals at Stations A-D during September 1978-May 1980. For simplicity 2 yr of data have been pooled and are presented on a single annual cycle.

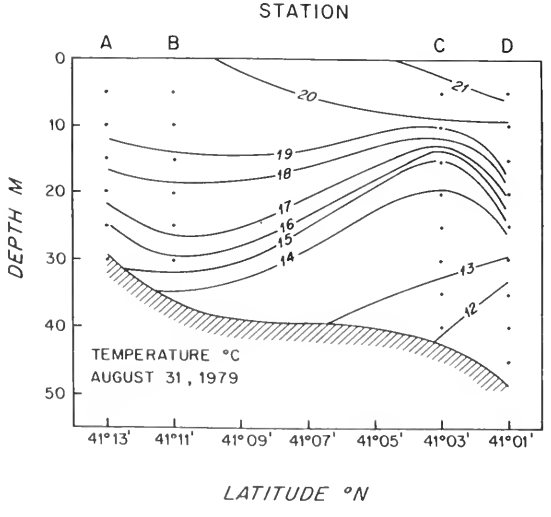

FIGURE 2.—Water column temperature structure along the transect from Stations A to D, 31 August 1979, illustrating the intense thermocline and its intersection with the bottom.

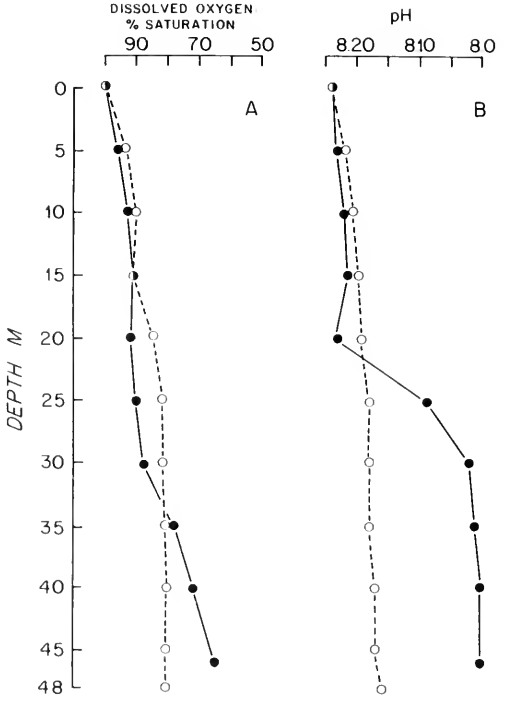

FIGURE 3.—Vertical profiles of percentage saturation of dissolved oxygen and pH at Station D for April (○) and August (●).

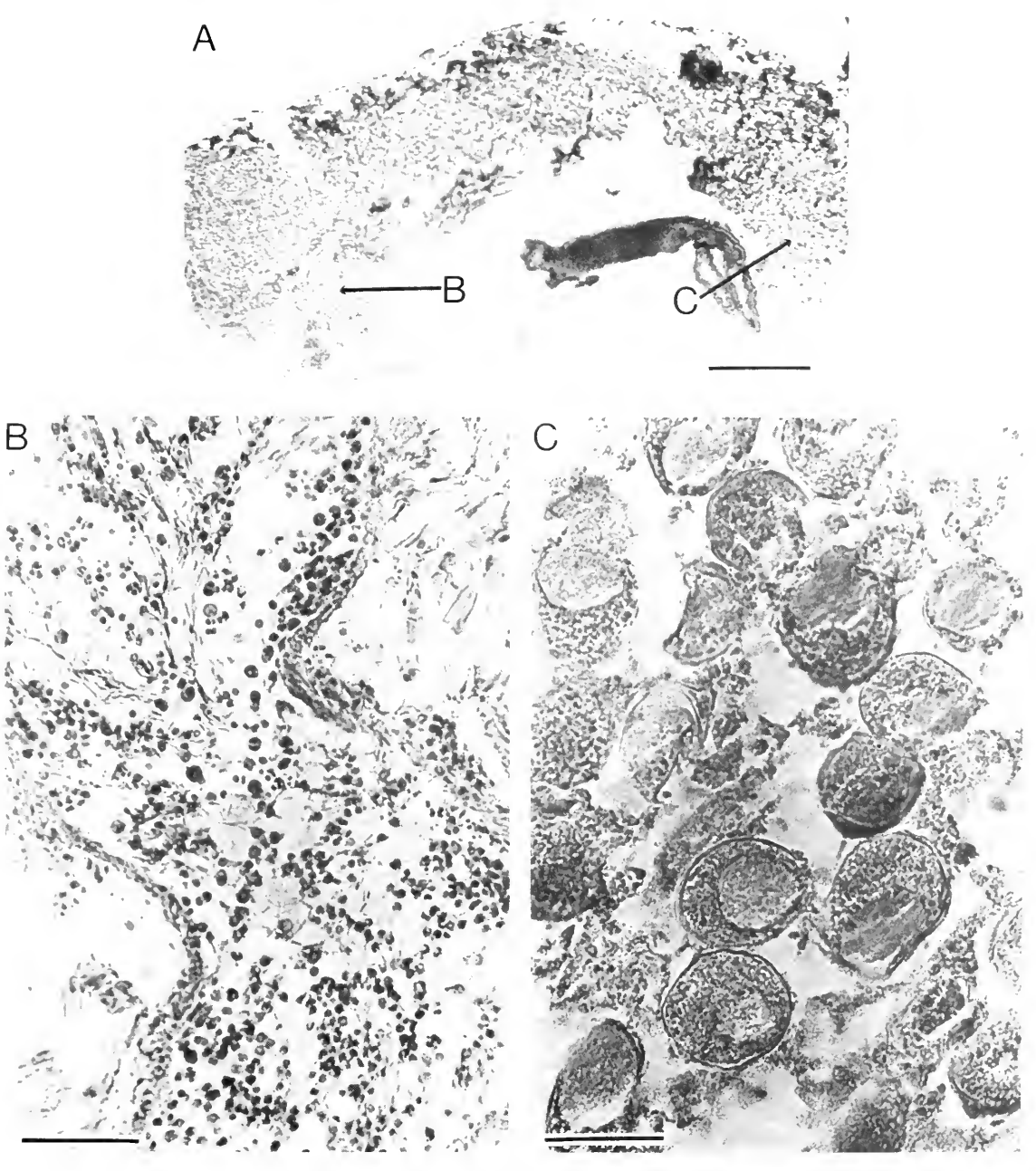

FIGURE 4.—Midventral sections of hermaphrodite *Arctica islandica* collected at Station A, 2 January 1980. A. Section illustrating spatially separate male (B) and female (C) gonadal tissue. Scale bar 1 mm. B. Expanded view of male gonadal tissue illustrating spent male follicle. Scale bar 50 μ. C. Expanded view of female gonadal tissue illustrating degenerating ova. Scale bar 50 μ.

ing during one annual cycle in either of the two years when observations were made. Gonadal maturation, then, probably occurs only once per year in each individual clam. The mean diameter of the ova taken from histological sections of ripe female clams was 52.4 μ ($n = 59$ ova). This compares with a value of 66.3 μ ($n = 22$ ova) obtained from unfertilized eggs stripped from ripe, live animals. The disparity between preserved and live material in the present instance is probably

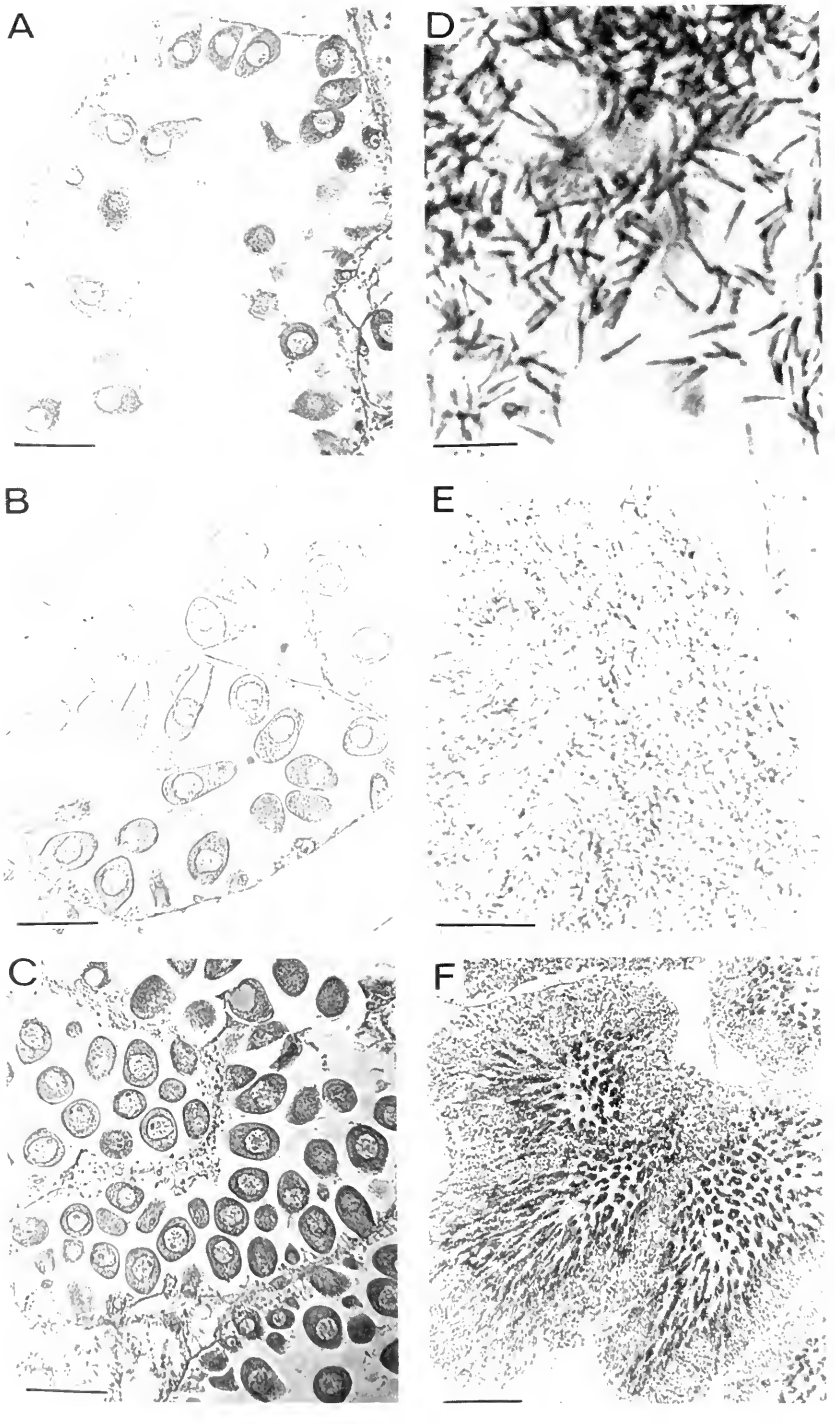

FIGURE 5.—Sequential development of gonadal material in the dorsal-ventral plane in *Arctica islandica*. A. Female, dorsal section, spent gonadal tissue. Scale bar 100 μ. B. Female, midventral section, partially spent gonadal tissue. Scale bar 100 μ. C. Female, ventral section, ripe gonadal tissue. Scale bar 100 μ. Preparations A-C from one clam. D. Male, dorsal section, ripe spermatozoa. Scale bar 10 μ. E. As for D except scale bar 50 μ. F. Male, ventral section, late active development. Scale bar 100 μ. Preparations E and F from one clam. Both clams from Station D, 15 June 1979.

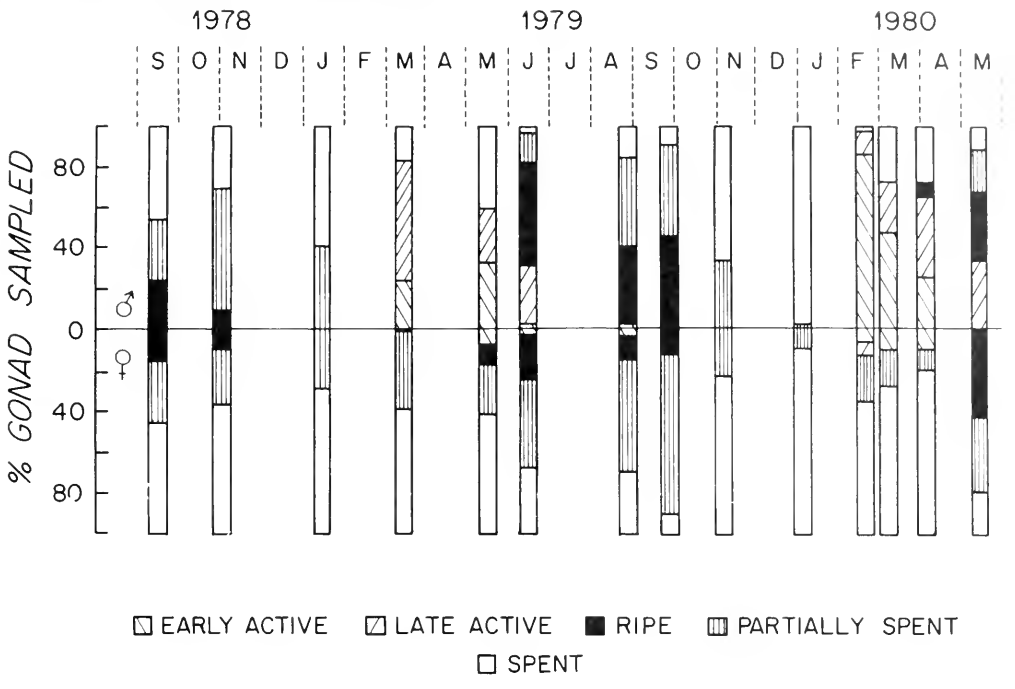

FIGURE 6.—Seasonal changes in gonadal development by sex in *Arctica islandica* for the period September 1978-May 1980; all stations pooled.

due to shrinkage during fixation and subsequent dehydration in alcohol. Both values are considerably lower than the diameter of 85-90 μ reported by Loosanoff (1953); however, these latter values were for fertilized eggs. Individual spermatozoa measured 6 μ in length in both fixed and live preparations.

Table 1 summarizes observed gonadal conditions in midventral sections taken from *A. islandica* at all stations during the study. Data are pooled for shallow (A and B) and deep (C and D) stations, respectively, due to the similarity of annual bottom temperature changes at these sites (Figs. 1, 2). Gonadal condition data are pooled for all stations and are presented graphically in Figure 6. Several major features were evident. Early active development in the male clams first occurred in early February and continued through May. Late active male development began in late February and remained evident until June. Most ripe males occurred from May through September and partially spent male clams were found from May through November and during January 1979. Eight percent of the female clams were in early active stage in May 1979. Two percent of the female clams were in late active stage in June and August 1979. Gametogenesis in the female clams began earlier in the year of 1980 than in 1979, with 12% of the females in early or late active stage in February 1980, and 10% in late active stage in both March and April 1980. Ripe females were present from May through October. The small proportion of early and late active females recorded during February to June in comparison to the larger equivalent proportion (31-93%) of males suggested that the duration of the period required to attain ripeness is shorter in the female clams.

The onset of spawning activity in both sexes was marked by a substantial increase in the proportion (to over 30% of total in both males and females) of partially spent animals and continued during the spawning period. Completely spent individuals were greatest from August through November, although some were found as early as May and June. In the female clams only partially spent and spent individuals were present year-round, the former being particularly abundant during August and September, and the latter being most abundant from November through March. A prolonged spawning period from May through November was indicated even though levels were low during the period May through July.

TABLE 1.—Numbers of *Arctica islandica* in each gonadal development stage by date for the period September 1978-May 1980: Data are pooled for shallow (A, B) and deep (C, D) stations, respectively. Stage description: EA, early active; LA, late active; R, ripe; PS, partially spent; S, spent.

			♂						♀					
Date	Station		EA	LA	R	PS	S	*n*	EA	LA	R	PS	S	*n*
9/78	A + B				2		2	4	1	2	1	1	1	6
	C + D				3	4	6	13			2	4	7	13
11/78	A + B					8	4	12			2	5	10	17
	C + D				3	9	5	17				1	5	6
1/79	A + B					2	3	5				4	11	15
	C + D	[1]												
3/79	A + B		3	7			2	12				5	8	13
	C + D	[1]												
5/79	A + B		8	6			10	24	1		1	3	8	13
	C + D	[1]												
6/79	A + B		1	11	27	11	4	54			11	16	17	44
	C + D			20	27	3		50		1	10	23	12	46
8/79	A + B				14	14	8	36			5	8	10	23
	C + D		1		10	14	2	27		1	1	21	6	29
9/79	A + B				1	4	1	6			1	3	1	5
	C + D				4	1		5				3		3
11/79	A + B					2	4	6				2	7	9
	C + D	[1]												
1/80	A + B						14	14				1	13	14
	C + D	[1]												
2/80	A + B		12	1			1	14	1	1		4	10	16
	C + D	[1]												
3/80	A + B		7	4			4	15	1			2	7	10
	C + D	[1]												
4/80	A + B	[2]												
	C + D		3	10	1		6	20	2			2	17	21
5/80	A + B			1	3	3		7			2	3		5
	C + D			4	2		2	8			4	3	3	10
Total								349						318

[1]Dredging prevented by bad weather.
[2]No collection due to gear failure.

A total of 667 *A. islandica* were of separate sexes and the observed ratio of this sample was 1:0.91. These data are not significantly different from a 1:1 sex ratio. This analysis omits the two hermaphrodites. Recently, Thompson et al. (1980b) have described the advanced age for sexual maturity in *A. islandica*, and Ropes and Murawski (1980) have examined the size and age at sexual maturity of *A. islandica* collected from a depth of 53-55 m south of Long Island, N.Y. They found that individual *A. islandica* as large as 47 mm in length had undifferentiated gonads and males began producing germinal cells at a smaller size and younger age than females. Small individuals were rare in the present study. *Arctica islandica* caught with the hydraulic dredge ranged from 70 to 110 mm in shell length, but were predominantly (84% of total) from 80 to 100 mm. The smallest specimen caught in the nonhydraulic dredge measured 62 mm in length, but most specimens (80% of total) were 80-100 mm. A record relating the length of each clam examined to its gonadal development was not kept in the present study; therefore a relationship between sex and length cannot be described. The present data on sex ratio differ from those of Jones (1980), who observed a sex ratio of 1:0.72 in a sample of 320 *A. islandica* of >75 mm individual length which were collected from offshore New Jersey during the period April 1977-March 1979.

DISCUSSION

Data describing water column physical characteristics are in general agreement with previous work in illustrating the seasonal, intense thermocline, and indicate that mixing across this phenomena is small during the summer months. Partial oxygen depletion below the thermocline during the summer is probably strongly related to biological activity.

The minor differences in gonadal development in *A. islandica* between stations is, at first, surprising considering the fact that the inshore, shallower stations (A and B) were consistently warmer than the offshore, deeper stations (C and D) (Figs. 1, 2, 6); however, an assessment of go-

nadal condition is subject to the following inherent inadequacies. First, a continuous gametogenic process is being described in discrete stages. Second, it is difficult to consistently obtain a midventral section that is a representative mean of the cline of gonadal developmental stages within one animal. Third, sample collections were relatively infrequent considering the small differential in bottom temperatures between the stations and the comparatively high rate of change of bottom temperature during the summer months (Fig. 1). It is probable that these three factors effectively combined to mask any depth-dependent difference in gonadal development.

Morphologically ripe specimens were present from March through October, but predominated from May through September. Although no morphologically ripe specimens were found in December or January—in contrast to the data of Loosanoff (1953)—the presence of partially spawned animals at this time, followed by the first appearance of early gametogenic stages in February and March, supports Loosanoff's hypothesis that no significant "resting" or "indifferent" period occurs in the annual gametogenic cycle. The sequential ripening of gonadal follicles from the hinge (dorsally) towards the foot (ventrally), in a manner similar to that described for *Mya arenaria* by Coe and Turner (1938), was not described by Loosanoff (1953). No examples of the "atypical" sperm development described by Loosanoff (1953) were observed in the present study. The present data are, however, not in complete agreement with the recent statement in Thompson, Jones, and Dreibelbis (1980), with respect to *A. islandica*, that "All individuals spawned once and once only in each of the two years studied." Jones (1980) is quoted as the source of documentation substantiating this statement. This is somewhat surprising in that, like the present study, Jones (1981) found some sequential gonadal development and the presence of a large proportion of partially spent individuals of both sexes in samples collected in the late summer and fall months. Both of these observations support the conclusion that individual specimens spawn at least once per annual reproductive cycle.

It is relevant to speculate on the nature of the proximal stimuli (sensu Baker 1938) of gametogenesis and spawning in *A. islandica*, given the present physical and biological data, based on the extensive discussion of the subject by Baker (1938) and Giese and Pearse (1974). *Arctica islandica* initiated gametogenesis in February when water temperature is lowest. This is in contrast to the more intensively studied intertidal species which either cease gametogenesis during the period of lowest temperature, e.g., *Mytilus edulis* in Northern Europe (Chipperfield 1953), or initiate gametogenesis only with rising water temperatures and at the time of the phytoplankton spring bloom, e.g., *Ostrea edulis* and *Crassostrea gigas* (Walne and Mann 1975). Ansell (1974), Gabbott (1975), and Mann (1979a, b) found that the initiation of gametogenesis in bivalves is often preceded by a period of accumulation of carbohydrate reserves which are subsequently used as a predominant respiratory substrate during gametogenesis and that this period of accumulation usually coincides with a period of high primary productivity and food availability. The author can find no data on seasonal phytoplankton productivity for the region immediately east and south of Block Island; however, substantial data are available for the lower Narragansett Bay (Hitchcock and Smayda 1977; Pratt 1965; Smayda 1957), Block Island Sound (Riley 1952b), and Long Island South (Smayda 1976). Lower Narragansett Bay is characterized by an intense winter (January to March) diatom bloom and a smaller, late summer to autumn (July to October) bloom (Smayda 1976). Block Island and Long Island Sounds exhibit a more classical spring and autumn bloom (Hitchcock and Smayda 1977; Smayda 1976). It is not unreasonable to suggest that phytoplankton from the autumn and winter blooms in Narragansett Bay are washed into Block Island Sound (Riley 1952a), and that, because of the vertically well-mixed nature of the water column at this time, both they and the phytoplankton from the classical spring and autumn blooms become available to *A. islandica*. Phytoplankton was probably made available by wind and storm events similar to those which effect the mixing and distribution of chlorophyll in the New York Bight and Georges Bank, as described by Walsh et al. (1978). In turn these blooms may be a potential food source for storage metabolism in *A. islandica* during the late fall, winter, and early spring months prior to and coincident with the initial stages of gametogenesis. Specimens collected throughout this period had both bright green digestive glands and a well-developed crystalline style indicative of active feeding on phytoplankton.

The precise nature of the spawning stimulus to *A. islandica* remains open to discussion. Loosanoff (1953) suggested that spawning was initiated at a water temperature of approximately 13.5°C; however, the data of Figures 1 and 6 indicate that absolute temperature per se is probably not the ultimate spawning stimulus. Furthermore, laboratory experiments to induce spawning by temperature shock alone have proved both inconsistent and usually unsuccessful (Loosanoff 1953; Landers 1976; Lutz et al. in press). Indeed, *A. islandica* has proven to be a very difficult species to spawn in laboratory systems. It also fails to respond to salinity and pH changes, the addition of suspension of sex products (Loosanoff 1953; Landers 1976), and the more recent method of Morse et al. (1977) involving exposure to alkaline seawater (pH = 9.1) and hydrogen peroxide (range of concentrations $2.5 - 5 \times 10^{-3}$ M) (Lutz et al. in press). While these methods of stimulating spawning have generally been very successful with many intertidal and shallow water species (Loosanoff and Davis 1963; Morse et al. 1977) which experience short-term (e.g., tidal) environmental fluctuations, their inapplicability to *A. islandica* is, perhaps, not surprising considering the fact that the deep, infaunal habitat of the species is comparatively well damped from short-term environmental fluctuations. Spawning occurred from May through November in field populations of *A. islandica*, and was heaviest during late August to October and at the time of the fall thermocline breakdown. Changes in bottom temperature coincidental with spawning occurred, but the rate and magnitude were small (Fig. 1). Clarke[4] recorded a prolonged spawning season for *A. islandica*. His studies of *A. islandica*, which were collected from a similar temperature regime to the present study in depths of 20 m off Seabrook, N.H., indicated some spawning from June through October with the greatest intensity from August to October. The prolonged nature of the spawning season in field populations reinforces the conclusion that while a specific, absolute temperature may be an important spawning stimulus, it is probably effective only in conjunction with changes in other stimuli, such as increases in percentage saturation of oxygen, pH, and food availability.

Spawning stimuli other than temperature have been reported by Ansell et al. (1978), who found a close correlation in the Clyde Sea area between an abrupt increase in bottom dissolved oxygen levels following a seasonal thermocline breakdown and spawning activity in the infaunal bivalve *Nuculana minuta*.

The fate of larval *A. islandica* spawned prior to the thermocline breakdown also remains open to discussion. The observations of Landers (1976), Wood and Hargis (1971), and Cragg and Gruffydd (1975) suggest that larvae in the early stages of development swim upwards and that substantial larval mortalities are probable from early spawnings, since, at least, temperatures too hot for survival would be encountered. To complete development successfully larvae spawned in June would have to remain below an intense thermocline through which little mixing occurs. This appears improbable. The inference is that a period exists during which the survival of larvae is limited by hydrographic events and that the larvae of *A. islandica* do not freely move throughout the entire depth of the water column until after the breakdown of the summer thermocline. Furthermore, the low winter water temperatures recorded in the Middle Atlantic Bight may also effectively depress continued development of larval stages spawned late in the fall months. Therefore the period during which the larvae of *A. islandica* survive to metamorphosis may be considerably shorter (approximately 2 mo, October and November) than that during which the adults are capable of spawning (7 mo, May to November).

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REGENERATION OF NITROGEN BY THE NEKTON AND ITS SIGNIFICANCE IN THE NORTHWEST AFRICA UPWELLING ECOSYSTEM

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ABSTRACT

Nitrogen and phosphorus excretion rates were measured for octopus and six species of fish in the northwest Africa upwelling region near lat. 21°40'N. The nekton excretion rates ranged from 0.44 to 4.61 μg NH_4-N/mg dry weight per day and the whole body C:N (by atoms) of the specimens was 4.85. The calculated nitrogen turnover time in the well-fed specimens was about 65 days. The estimated rates of ammonium regeneration over the shelf (<200 m) for all the nekton was about 3 mg-at/m^2 per day which was 27% of the phytoplankton ammonium uptake requirements. On the slope (>200 m) the nekton regenerated 1.8 mg-at/m^2 per day which was 11% of phytoplankton ammonium uptake. The ammonium production by bacterioplankton, zooplankton, nekton, and sediments accounted for 226% of the ammonium utilized in the nearshore shelf region and 83% in the offshore region.

Ammonium is an important source of nitrogen for phytoplankton growing in the sea. Estimates of nutrient uptake using ^{15}N tracer experiments have indicated that ammonium regeneration may be responsible for 44 to 83% of nitrogen utilized by phytoplankton in the North Pacific gyre (Eppley et al. 1973) and up to 50% in the Peru upwelling system (Dugdale and Goering 1970). The source of ammonium in the marine environment may be recycled through any of several animal groups. Ammonium regeneration in Long Island Sound was found to be predominantly from zooplankton and benthos (Harris 1959), while in Georgia coastal waters, phosphate regeneration (and presumably ammonium regeneration) was produced by zooplankton that are large enough to be sampled adequately by nets (Pomeroy et al. 1963).

The regeneration of nitrogen by zooplankton has been examined in several coastal upwelling ecosystems. The red crab, *Pleuroncodes planipes*, copepodites, and adult *Acartia* regenerated about 16% of total phytoplankton nitrogen uptake (Whitledge in press) in the Baja California upwelling system while zooplankton in the Peru upwelling ecosystem regenerated about 15% of total nitrogen uptake (Whitledge 1978). In the northwest Africa upwelling region off Cape Blanc (Fig. 1), the zooplankton were shown to recycle 33% of nitrogen productivity over the shelf (Smith and Whitledge 1977).

The focus in most regeneration studies has been zooplankton because fish and benthic organisms have relatively smaller biomasses in many oceanic areas. However, the biomass of the anchoveta in the Peru upwelling ecosystem was estimated to be 15 times greater than the zooplankton biomass (Dugdale and Goering 1970), and the fish regenerated 22% of the phytoplankton total nitrogen uptake and 59% of the ammonium uptake (Whitledge 1978). Since the fish in the Peru upwelling system produce a significant quantity of recycled nitrogen, another major fishing area, the northwest Africa upwelling system, was studied to examine the relative importance of nutrients regenerated by fish in comparison with that by zooplankton (Smith and Whitledge 1977), benthic processes (Rowe et al. 1977), and bacterioplankton (Watson 1978). In addition, the biology of many species of fish has not been investigated with respect to changes of nitrogen excretion rates over time and under various conditions so an attempt was made to increase our understanding of this elimination process.

METHODS

Near-bottom fish specimens of *Diplodus senegalensis*, *Pegellus couperi*, *Cantharus cantharus*, and *Pomadasys incisus* were captured in bottom

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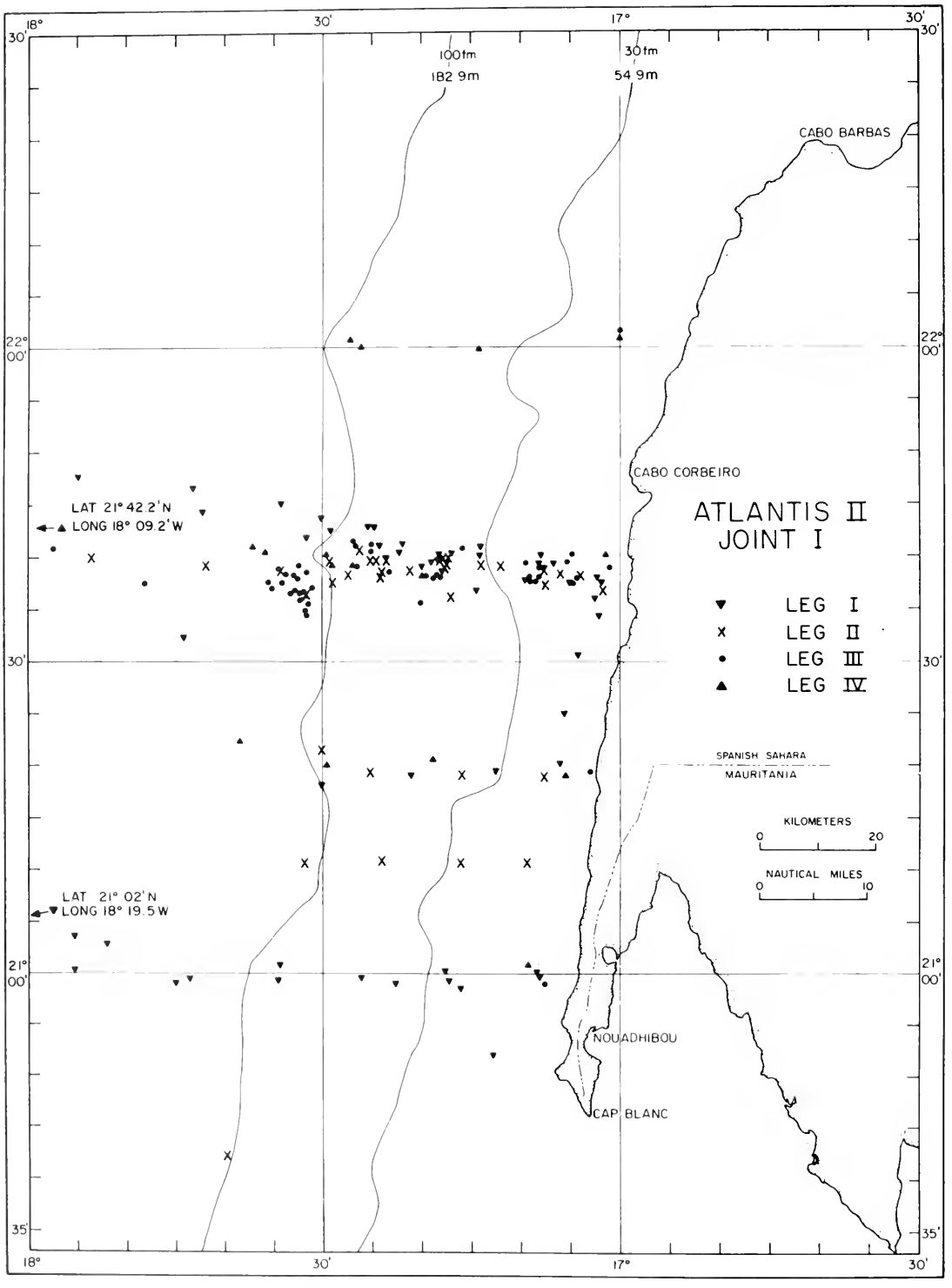

FIGURE 1.—Station locations in the upwelling region off northwest Africa.

trawls. The fish were transferred immediately to a holding tank aboard the RV *Atlantis II* and were maintained as long as a week with daily feeding. Specimens were held at least 6 h before experiments were initiated. Excretion measurements were collected on several specimens after the holding tank had been cleaned, rinsed with ethyl alcohol, flushed, and filled with seawater. The tank was covered with black polyethylene sheeting to reduce light and to prevent contamination by particulate matter. After the animals were placed in the tank and the experiment was initiated, water samples were collected every 10 min for periods of up to 3 h. Most of the experiments were started in the late evening so the temperature of the experimental tanks was within 1°-2°C of ambient surface seawater. There was no heating effect by sunlight so the temperature ranged from 14.5° to 16°C for all the experiments with <0.5° change in temperature during any of the experiments. "Fresh" specimens were examined within 12 h of capture. Specimens that had been starved for 1 and 2 d were used to estimate nonfeeding excretion rates. After all water samples had been collected, the specimens were blotted on towels and weighed. The animals were subsequently dried in a circulating oven at 70°C until a constant dry weight was obtained. The whole dried fish were ground into a powder for determination of percentage body nitrogen and carbon.

Excretion samples were analyzed for ammonium, urea, nitrate, silicate, phosphate, dissolved organic nitrogen, and dissolved organic phosphorus. The samples were freshly run and were filtered through a 0.45 μm glass-fiber filter to remove particulate matter. The chemical methods used were similar to those described by Freiderich and Whitledge (1972) except for urea and dissolved organic nitrogen and phosphorus which were determined by the methods of DeManche et al. (1973) and Armstrong et al. (1966).

RESULTS

Excretion Measurements

Eight excretion experiments were performed on a total of five species of demersal fish. In addition, excretion measurements were taken from two blue sharks, *Prionace glauca*, and several octopi, *Octopus vulgaris*. The typical tank concentrations of nitrogen compounds measured during the experiments are shown in Figure 2. The rate of ammonium excretion was approximately twice as large as the rate for urea. The rate of excretion for ammonium was more nearly linear than that for urea, although the nonlinearity for urea is probably within the precision limits of the method. The sum of ammonium and urea represents the identified nitrogen excretion in the experiments. The difference between this sum of ammonium and urea and total nitrogen excretion (as measured after ultraviolet irradiation) is probably composed of organic nitrogen compounds such as dissolved amino acids, trimethylamine oxide (Grollman 1929; Wood 1958), or creatine (Whitledge and Dugdale 1972). All experiments conducted showed a nearly linear increase in ammonium concentrations over the short duration of the experimental periods. Likewise the increases in urea and total excreted nitrogen were nearly linear but were more variable than ammonium.

A summary of all nitrogen excretion experiments is shown in Table 1. Well-fed demersal species such as *Diplodus senegalensis* excreted from 1.03 to 1.44 μg NH_4-N/mg dry weight per

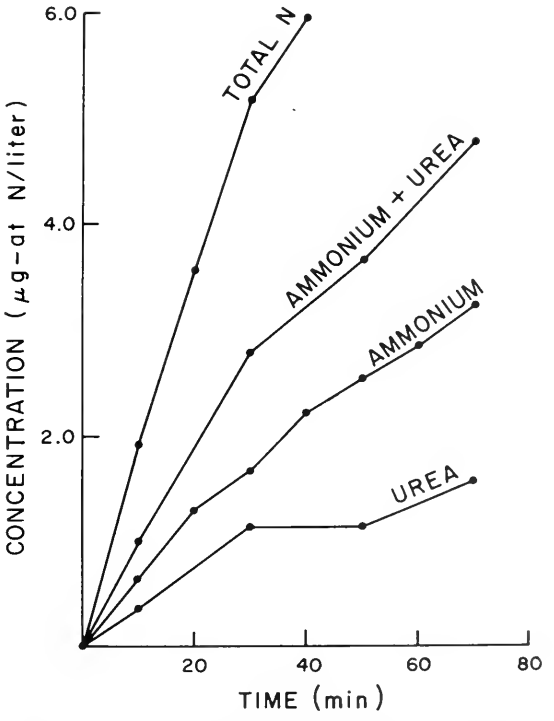

FIGURE 2.—Tank concentrations of ammonium, urea, and total nitrogen as measured by ultraviolet irradiation during an excretion experiment.

TABLE 1.—Excretion rate measurements of specimens from northwest Africa.

No. of individuals	Specimens	Experimental condition	μg N/mg dry wt per day			μg P/mg dry wt per day	
			NH_4	Urea	DON	PO_4	DOP
12	*Diplodus senegalensis*	fresh	1.44	0.76	2.6	0.23	0.09
9	*Diplodus senegalensis*	starved, 1 d	0.90	0.26	—	0.15	0.04
6	*Diplodus senegalensis*	starved, 2 d	0.64	0.35	2.0	0.22	0.18
2	*Pagellus couperi* and						
1	*Cantharus cantharus*	fresh	0.91	—	1.0	0.12	0.04
2	*Pagellus couperi* and						
1	*Cantharus cantharus*	starved, 1 d	0.64	0.08	—	0.05	—
1	*Pomadasys incisus* and						
9	*Diplodus senegalensis*	fresh	1.22	0.33	1.6	0.18	0.05
2	*Prionace glauca*	fresh	0.44	0.55	0.93	0.08	0
4	*Octopus vulgaris*	fresh	0.78	0.11	—	0.42	—
5	*Sardinella* spp.	fresh	4.61	4.78	—	1.68	—

day and 0.31 to 0.76 μg urea-N/mg dry weight per day. Specimens starved 24 h excreted 0.90 and 0.26 μg NH_4-N and urea-N/mg dry weight per day. A 2-d starvation lowered ammonium excretion to 0.64 while urea was 0.35 μg urea-N/mg dry weight per day. These rates are somewhat higher than the means of 0.17 and 0.05 μg N/mg dry weight per day for ammonium and urea measured at 12°C for Pacific staghorn sculpin, *Leptocottus armatus*; starry flounder, *Platichthys stellatus*; and blue sea perch, *Taeniotoca lateralis* (Wood 1958). After temperature corrections are made using a Q_{10} of 2.0 these rates are still larger than those measured by Wood (1958). Although linear temperature adjustments can be estimated, the food conversion efficiency can be variable and cannot be estimated by simple increases in rates as temperature increases (Pandian 1970); therefore, excretion rates can be expected to be somewhat nonlinear also. Feeding studies on the Atlantic menhaden showed that ingestion rates are equivalent to 0.30-1.2 μg N/mg dry weight per day for filter feeding on *Thalassiosira rotula* (Durbin and Durbin 1975). Using an assimilation efficiency of 80% and growth rate of 5% assimilation, the nitrogen excretion rates should be about 0.23 μg N/mg dry weight per day. This rate is about 20 to 33% of the rates calculated for the smaller specimens in this study.

The other demersal species, *P. coupei* and *C. cantharus*, excreted 0.91 μg NH_4-N/mg dry weight per day when specimens were fresh and 0.64 μg NH_4-N/mg dry weight per day when starved 48 h. The pelagic *Sardinella* spp. showed an ammonium excretion rate of 4.61 μg NH_4/mg dry weight per day. Ammonium excretion by the blue shark was 0.11 μg N/mg dry weight per day while urea excretion rates were slightly higher (0.13 μg N/mg dry weight per day) than values for the demersal fish.

Measured quantities of orthophosphate in excretion samples were smaller than ammonium but displayed an approximate linear increase with time. Dissolved organic phosphorus (DOP) was often excreted in quantities similar to orthophosphate. The sum of orthophosphate and DOP, representing total phosphorus excretion, is a linear function of time over the relatively short experimental period (Fig. 3). Phosphorus excretion rates (Table 1) were smaller after the fish had been starved 1 d. However, specimens starved 2 d showed high phosphorus excretion rates. Ammonium was decreased after 2 d of starvation, indicating elemental excretion ratios may change as starvation proceeds. Nitrate, nitrite, and silicate were excreted in insignificant or zero concentrations in all experiments. Control chambers starting with the same initial water as the experimental tanks showed no con-

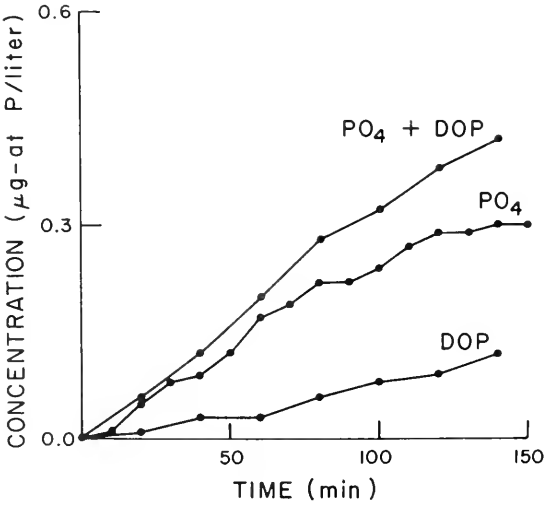

FIGURE 3.—Tank concentration of orthophosphate and dissolved organic phosphate during an excretion experiment.

centration changes of any of the measured parameters greater than the standard precision of the chemical methods (≈5%).

Other Measurements

The wet and dry weights were determined for all specimens except for *P. glaucas* where only wet weights were estimated by displacement volume. The wet and dry weights determined for all other specimens (Fig. 4) were linearly related by the least squares equation, dry weight = 0.284 wet weight + 1.5, with an r^2 of 0.96.

The percentage body carbon content in all dried specimens ranged from 33.7 to 48.9. The mean and standard deviation for the 34 samples was 41.6±4.24% C. Fresh *D. senegalensis* specimens contained a mean of 42.59% C (Table 2) while specimens starved 1 and 2 d had 43.08 and 36.6% C. The mean percentage body nitrogen determined for all specimens was 9.35 with a standard deviation of ±1.49%. Fresh *D. senegalensis* specimens contained 10.36% N while specimens starved 1 and 2 d had 9.79 and 7.41% N. Carbon to nitrogen ratios (by atoms) calculated from these data were 4.85 for fresh *D. senegalensis* and 5.18 and 5.90 for specimens starved 1 and 2 d. These ratios show a larger loss of nitrogen than carbon during starvation and the ratios bracket the value of 5.17 measured as the mean C:N of 10 Peruvian anchoveta, *Engraulis ringens*, and correspond to the C/N values reported for phytoplankton and zooplankton (Walsh and Howe 1976). When changes in body nitrogen content are calculated from changes in C/N values and are compared with measured nitrogen excretion losses, assuming defecation is approximately equal to excretion (an assimilation efficiency of 50%), then about 67% of the observed C/N changes in *D. senegalensis* are explained.

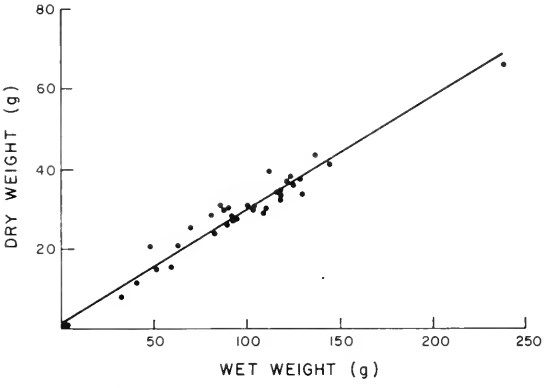

FIGURE 4.—Wet weight vs. dry weight plot for all fish specimens.

The absolute rates of nitrogen loss by excretion were calculated for the various nitrogen fractions. The sum of ammonium and urea losses were then compared with body nitrogen content to determine percentage body nitrogen loss per day which ranged from 1.2 to 1.5%. These nitrogen loss rates would require from 65 to 85 d for turnover of body nitrogen. These nitrogen turnover estimates are quite reasonable for fish of this size range so the nitrogen excretion rates should not be grossly overestimated due to the stress of capture and handling. Of course, loss of scales, mucus, and reproductive losses would decrease this turnover time and, if they were known, would represent a refinement of this estimate.

Nekton Biomass

Nekton biomass was determined in the study area by acoustic mapping surveys on the RV *Atlantis II* and bottom trawls during the cruise period. Results of the acoustic surveys that were

TABLE 2.—Mean and standard deviation of experimental measurements for *Diplodus senegalensis*, *Octopus vulgaris*, and *Prionace glauca*.

Specimens[1]	Dry wt (g)	Body C (% of dry wt)	Body N (% of dry wt)	Body C/N (by atoms)	NH_4 excretion/day (g)	Urea excretion/day (g)	Sum NH_4 + urea excretion/day (g)	Total N excretion/day (g)	Body N excreted/day as NH_4 and urea (%)	Turnover time of body N (d)
D. senegalensis fresh	29.42 (6.13)	42.59 (3.84)	10.36 (1.08)	4.85 (0.77)	0.0359	0.0100	0.0459	—	1.53	65.4
D. senegalensis starved 1 d	27.27 (6.41)	43.08 (4.40)	9.79 (1.07)	5.18 (0.73)	0.0245	0.0071	0.0316	—	1.17	85.5
D. senegalensis starved 2 d	28.36 (4.87)	36.60 (3.57)	7.41 (0.52)	5.90 (0.75)	0.0182	0.0100	0.0282	0.0569	1.34	74.6
O. vulgaris fresh	318.5		11.04		0.248	0.035	0.283	—	0.805	124
P. glauca fresh	2,160	—	—	—	0.950	1.188	2.138	—	0.989	101

[1]Number of specimens as in Table 1.

coincident in time with the excretion experiments showed a mean pelagic biomass over the northwest Africa shelf of 40 to 60 g wet weight/m^2 (Thorne et al. 1977). Analysis of fish egg and larvae samples later indicated that the relative abundance of sardine to anchovy was about 4:1 (Blackburn and Nellen 1976) or mean densities of 32 g wet weight of sardines and 8 g wet weight of anchovy/m^2. Converting to dry weight the sardine and anchovy standing stock would be 8 and 2 g/m^2, respectively.

Demersal fish stocks on the shelf sampled by bottom trawling gear were more varied in composition than pelagic stocks. A composite estimate of demersal stocks taken in several trawls by three vessels included 2.2 g wet weight/m^2 of fish mainly represented by the families Sparidae, Sciaenidae, Pomadasyidae, and Congridae (Haedrich et al. 1976). In addition, at depths of about 50 m cephalopods were found in abundances of about 1 g wet weight/m^2, and at 200 m large numbers of the shrimp *Plesionika* spp. were collected, amounting to 1.44 g wet weight/m^2.

The biomass of pelagic fish in the slope area at depths >200 m was estimated by acoustic measurements to be about 80 g wet weight/m^2 and was thought to be composed of jack mackerel, *Trachurus symmetricus* (Thorne et al. 1977). Just offshore of the shelf break concentrations as large as 105 g wet weight/m^2 of fish were occasionally observed. Demersal fish biomass was smaller than found on the shallow shelf region and was estimated to be 3.3 g wet weight/m^2 from bottom trawls (Haedrich et al. 1976).

It should be noted that biomass estimates obtained from the acoustic survey for the pelagic populations and the trawl sampling for demersal nekton were often highly variable (Thorne et al. 1977). Several of the most abundant nekton species (e.g., *Sardinella* spp.) were migrating through the study area and a considerable amount of commercial fishing was occurring so the mean biomass values used in regeneration calculation are an attempt to use a reasonable value that was the best estimate of the nekton biomass assessment investigators.

Regeneration Rates

Regeneration rates were calculated from nekton biomass and fish excretion data for the shelf (<200 m) and slope region (>200 m) in the northwest Africa upwelling area. These regions were considered separately because of large differences in both the fish and zooplankton populations in these two areas. The sum of ammonium regeneration rates calculated for pelagic fish over the shelf amounts to 2.87 mg-at/m^2 per day (Table 3) while demersal fish regeneration rates were 0.09 mg-at/m^2 per day for a total of 2.96 mg-at/m^2 per day. The anchovy excretion rates were estimated from *Engraulis ringens* and *E. mordax* values (Whitledge 1978) and *Plesionika* spp. excretion rates were estimated using values for small sizes of *Pleuroncodes planipes*, a pelagic crab endemic to the eastern tropical Pacific.

The ammonium regeneration rates for the slope region were dominated by *T. symmetricus* (1.80 mg-at/m^2 per day) while demersal fish contributed only 0.04 mg-at/m^2 per day. The jack mackerel excretion rate used in the calculation was obtained from specimens examined in the eastern Pacific region (McCarthy and Whitledge 1972).

TABLE 3.—Regeneration of ammonium by fish over the shelf and slope areas of northwest Africa upwelling ecosystem.

	Wet wt g/m^2	Dry wt g/m^2	Ammonium excretion rate μg N/mg dry wt per day	Regeneration rate mg-at N/m^2 per day
Shelf (<200 m)				
Pelagic				
Sardine	32	8	4.6	2.63
Anchovy	8	2	[1]1.7	0.24
Demersal				
Sparids and flatfish	2.2	0.55	1.23	0.05
Cephalopods	1.0	0.17	0.71	0.01
Shrimp	1.4	0.22	[2]2.0	0.03
Total	44.6	10.94		2.96
Slope (>200 m)				
Pelagic				
Horse mackerel	80	20	1.26	1.80
Demersal				
Sparids	1.6	0.4	1.23	0.04
Total	81.6	20.4		1.84

[1]Estimated from *Engraulis ringens* and *E. mordax* rates.
[2]Estimated from *Pleuroncodes planipes* rates.

DISCUSSION

The significance of nutrient regeneration by fish is most apparent when the ammonium regeneration rates are compared with phytoplankton uptake rates measured by ^{15}N-labeled nitrate and ammonium. The mean ammonium and nitrate uptakes are estimated to be 11 and 10 mg-at/m^2 per day for the shelf region (MacIssac and Dugdale[2]). The ammonium regeneration rate for

[2]Jane J. MacIsaac and Richard C. Dugdale, University of Southern California, Los Angeles, CA 90007, pers. commun. June 1977.

the fish totals 2.96 mg-at/m^2 per day (Table 4), which is about 26.9% of the ammonium used by phytoplankton and 14.1% of total inorganic nitrogen utilized.

Results of zooplankton regeneration experiments obtained at the same time showed variations related to size of the organisms and depth of water. Smaller zooplankton were most abundant and had largest excretion rates inshore while the largest zooplankton biomass was located just offshore of the shelf break where the larger zooplankton with smaller excretion rates were found (Smith and Whitledge 1977). The mean ammonium regeneration rate calculated from zooplankton that were separated into four size classes of 102, 223, 505, and 1,000 μm was 4.7 mg-at/m^2 per day over the shelf, which is about 42.7% of the ammonium used in primary production and 22.4% of total inorganic nitrogen uptake.

The release of ammonium from the sediments off northwest Africa was estimated by placing bell jars on the bottom in the shallow inshore region (25 m) where divers could collect initial and final samples using plastic bottles (Rowe et al. 1977). The mean ammonium release rate from the two locations was 5.64 mg-at N/m^2 per day. This value represents 0.23 μg-at/l per day if mixing occurred over the entire water column in the nearshore region. The ammonium content of pore water in the upper few centimeters and at the seawater-sediment interface was quite large in the two nearshore stations compared with samples collected at 50 and 200 m. Likewise the gradients of ammonium production at the sediment-water interface was shown to decrease from >100 μg-at/l per cm at 25 m to <40 μg-at/l per cm offshore of the shelf break. So using the concentration of ammonium in pore water and sediment-water interface gradients as indicators of ammonium flux from the sediments, the sediments were estimated to be releasing about 5.6 and 1.9 mg-at/m^2 per day at water depths of 50 and 200 m. These sediment-release values would provide 78.9% of ammonium used in primary production and 24.2% of the total inorganic nitrogen uptake over the inner shelf. A smaller portion of productivity evidently sinks to the sediments hence smaller benthic release rates are observed.

The input to the water column from the sediments nearshore at depths of 30 m or less are probably very significant in creating and maintaining a high concentration of ammonium found in the shallow waters (Fig. 5) that are often discolored due to a large air-derived suspended load. The ammonium-release rates from the sediment are larger than nearshore pelagic regeneration rates and the large aeolian sediment load (Sarnthein and Walger 1974; Rowe et al. 1977; Milliman 1977) was presumably large enough to inhibit phytoplankton nutrient uptake as a result of light attenuation and to discourage large biomasses of zooplankton (Codispoti and Friederich 1978). It is therefore probable that the primary productivity not eaten by the small-sized zooplankton falls to the bottom, so an appreciable quantity of ammonium is placed in the water column by zooplankton excretion and particulate organic matter decomposition on the bottom.

TABLE 4.—Nitrogen budget for northwest Africa upwelling ecosystem.

	Ammonium regeneration mg-at/m^2 per day	Percent of ammonium uptake	Percent of nitrate plus ammonium uptake
Shelf[1]			
Bacterioplankton	0.5	7	2
Zooplankton	7.82	104	33
Fish	2.96	39	13
Benthic sediments	5.64	75	24
Total	16.92	225	72
Offshore[2]			
Bacterioplankton	4.43	27	20
Zooplankton	5.35	33	24
Fish	1.84	11	8
Benthic sediments	1.88	12	8
Total	13.50	83	60

[1]Phytoplankton ammonium uptake = 7.5 mg-at/m^2 per day.
Phytoplankton nitrate uptake = 16.0 mg-at/m^2 per day.
[2]Phytoplankton ammonium uptake = 16.2 mg-at/m^2 per day.
Phytoplankton nitrate uptake = 6.2 mg-at/m^2 per day.
Source for footnotes 1 and 2: Dugdale and MacIsaac, unpubl. results.

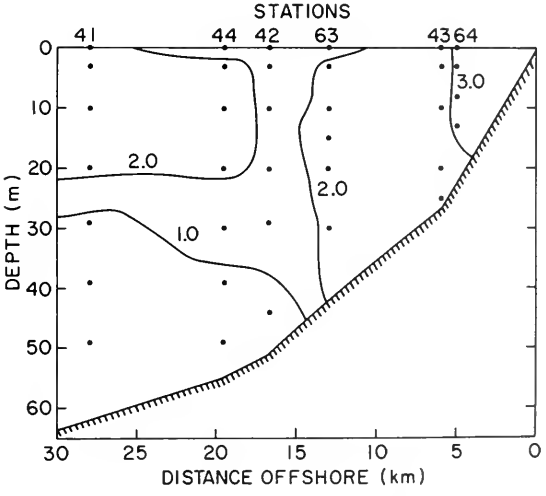

FIGURE 5.—Distribution of ammonium (μg-at/l) observed in a transect of stations across to shelf at lat. 21°40'N.

Bacterioplankton studies in the northwest Africa upwelling ecosystem (Watson 1978) estimated the phytoplankton biomass in the water column to be much larger than bacterial biomass at stations <350 m water depth. The bacterial biomass in the sediments, however, was higher nearshore and lower offshore. The water column contained only 8% of the bacterial biomass on the inshore stations, so the bacteria are probably recycling only about 0.5 mg-at N/m^2 per day inshore. The offshore region has about 73% of the bacterial biomass in the water column compared with the sediments, so the bacterioplankton may regenerate as much as 4.4 mg-at/m^2 per day in the deeper waters of 200 m or greater. The bacterial processes that were occurring in the sediments were estimated from bell jar experiments (Rowe et al. 1977). The inshore bottom ammonium release rates (5.64 mg-at/m^2 per day) include bacterial, meiofaunal, and chemical processes occurring in the sediments, so these values were used rather than the purely bacterial rates of Watson (1978). The difference between the bell jar and bacteria-only rates is about 5.1 mg-at/m^2 per day. This difference is quite high to explain as a chemical rate so meiofaunal rates evidently are quite important. In offshore waters the sediment release rates are much lower than inshore based on near-bottom ammonium gradients and decreased ammonium pore water concentrations.

The sparids in this study, Mediterranean Sea reef fish (Whitledge 1972), and the nearshore and bottom fish of British Columbia (Wood 1958) have apparently much smaller weight-specific ammonium excretion rates than fish such as the Peruvian anchovy, northern anchovy, jack mackerel, and sardinella. The increased metabolic rate needed by mackerels and clupeoids is probably a result of their large energy demands resulting from continuous swimming. Low metabolic rates in sluggish mammals have been shown to be related to their relatively infrequent movements (Whittow 1977) compared with highly active animals of similar body weight. As a result it could be predicted that respiration or excretion rates for fish should be related to both their body weight and index of locomotion such as swimming speed or daily swimming time.

The total amount of ammonium regenerated in the upwelling ecosystem off northwest Africa has spatial variability which cannot be ignored. Nevertheless, regeneration in organisms from bacterioplankton through benthos (Table 4) is estimated to recycle significantly large amounts of nitrogen in the ecosystem and easily produce all of the ammonium used in primary productivity. In some shallow locations ammonium is produced in large quantities and biological uptake is reduced such that high concentrations of ammonium are often observed in the very nearshore water.

ACKNOWLEDGMENTS

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THE ATLANTIC STURGEON, *ACIPENSER OXYRHYNCHUS*, IN THE DELAWARE RIVER ESTUARY

HAROLD M. BRUNDAGE III AND ROBERT E. MEADOWS[1]

ABSTRACT

Records of Atlantic sturgeon, *Acipenser oxyrhynchus*, captured in the Delaware River estuary from 1958 through 1980 were obtained from the literature, unpublished data, and logs maintained by commercial fishermen who took Atlantic sturgeon incidental to their operations for other species. During the period reviewed, there were 130 Atlantic sturgeon reported captured; 64 in commercially fished gill nets and 66 incidental to fishery and ecological studies. Atlantic sturgeon were most abundant in Delaware Bay (river km 0-55) in spring and in the lower tidal river (river km 56-127) during summer. This seasonal distribution appeared similar to that described for the Hudson River estuary. Atlantic sturgeon between 800 and 1,300 mm total length were relatively more abundant in the Delaware River estuary than had been reported in other estuaries, suggesting utilization of the Delaware system during a greater portion of the life cycle.

The Atlantic sturgeon, *Acipenser oxyrhynchus*, inhabits large estuaries and Atlantic coastal waters from Labrador to eastern Florida; a southern subspecies, *A. o. desotoi*, occurs throughout the Gulf of Mexico (Vladykov and Greeley 1963).

The Delaware River estuary, historically one of the major spawning and nursery areas for the Atlantic sturgeon, once supported the largest and most profitable sturgeon fishery on the Atlantic coast (Ryder 1890). The fishery in the Delaware River estuary was extremely short lived, however, and followed a pattern of rapid decline observed in most other estuaries. The commercial fishery, which began in the mid-19th century and expanded rapidly after 1870 as smoked sturgeon and caviar gained acceptance, declined precipitously about 1900 and virtually collapsed by 1905 as the population declined (see Ryder 1890; Cobb 1900; Murawski and Pacheco 1977).

Overfishing of adults on the spawning grounds combined with late maturity appears principally responsible for this decline, although destruction of benthic food organisms by coal silt pollution and general deterioration of water quality and destruction of juvenile Atlantic sturgeon by American shad, *Alosa sapidissima*, fishermen probably contributed.

Little is known of the present status of the Atlantic sturgeon in the Delaware River estuary. As a preliminary step towards an assessment all available recent records of Atlantic sturgeon capture in the estuary were compiled. Reliable, quantitative data were found for the period 1958 through 1980. Most records were obtained from the substantial body of published and unpublished data generated by recent fishery and ecological studies. Further information was obtained via personal communication with the staffs of the Delaware River Anadromous Fishery Project of the U.S. Fish and Wildlife Service, the Delaware Division of Fish and Wildlife, and Ichthyological Associates, Inc. In addition, during spring 1979 and 1980, three commercial gill netters who had previously worked with the authors maintained logs of Atlantic sturgeon captured incidental to their operations for other species. Some 25 other fishermen were interviewed to obtain their impressions of Atlantic sturgeon occurrence and abundance. Inherent in this approach was the premise that representative trends might become apparent when a body of incidental records and anecdotal accounts are considered together. Apparent trends must be interpreted cautiously, however, since sampling gear and effort varied considerably between and within years.

To aid in the delineation of spatial-temporal trends the estuary was divided into three regions based on physiography and salinity regime. "Delaware Bay" extends from the mouth (river km 0) to the vicinity of the Leipsic River (river km 55), is shaped like a flattened funnel and has

[1]Ichthyological Associates, Inc., 100 South Cass Street, Middletown, DE 19709.

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extensive shoals along the New Jersey shore (Fig. 1). The estuary narrows considerably at about river km 56 to form the "lower tidal river" which extends to Marcus Hook, Pa. (river km 127). The "upper tidal river" extends to the fall line just north of Trenton, N.J. (river km 222). Delaware Bay is generally polyhaline (18-30‰), the lower tidal river mesohaline to oligohaline (0.5-18‰), and the upper tidal river limnetic (0.0-0.5‰) (Tudor 1980). These zones of salinity may be displaced considerably, however, depending upon freshwater flow, tidal stage, and local meteorological conditions.

RESULTS

From 1958 to 1980 there were 130 documented captures of Atlantic sturgeon in the Delaware River estuary (Table 1, Fig. 1); 68 in Delaware

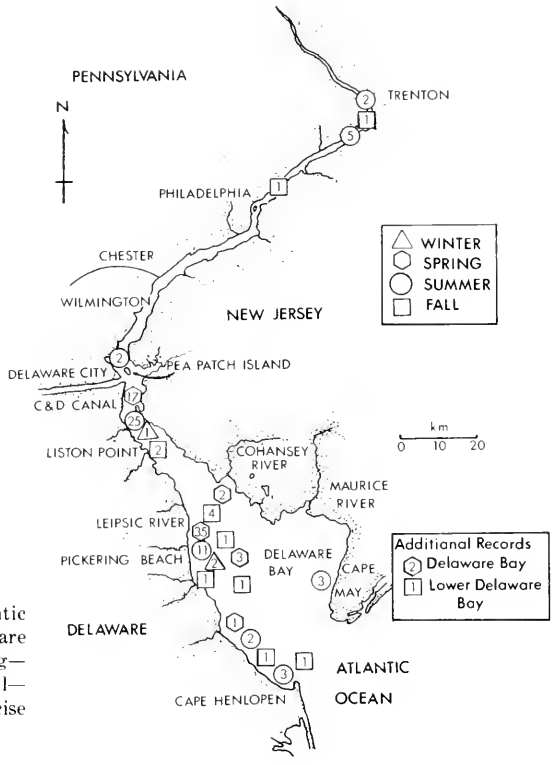

FIGURE 1.—Locations of recorded captures of Atlantic sturgeon in the Delaware River Estuary, 1958-80. Seasons are defined as winter—December through January; spring—March through May; summer—June through August; fall—September through November. Records for which precise capture locations are not known are also given.

TABLE 1.—Recorded captures of Atlantic sturgeon, *Acipenser oxyrhynchus*, in the Delaware River estuary, November 1958-July 1980.

Date	Area	River km	Salinity ‰	Temp. (°C)	Method of capture	No.	Total length (mm)	Source
14 Nov. 1958	Lower Delaware Bay	—	—	—	9.1 m trawl	1	508	de Sylva et al. 1962
Sept. 1967	Harbor of Refuge, Del.	3	—	—	9.1 m trawl	1	—	Daiber and Wockley 1968
Oct.	Joe Flogger Shoal, Del.	42	—	—	9.1 m trawl	1	—	Daiber and Wockley 1968
31 July 1968	Liston Point, Del.	77	—	—	28 cm gill net	5	814, 1,143, 1,165, 1,193, 1,431	IA, Inc.,[1] Middletown, Del.
1 Aug.	Liston Point	77	—	—	28 cm gill net	5	680, 1,157, 1,172, 1,323, 1,431	IA, Inc., Middletown
9 Aug.	Liston Point	77	—	—	28 cm gill net	1	889	IA, Inc., Middletown
Mar.-Apr. 1969	Little River, Del.	45	—	—	13-14 cm gill net	5	—	DRBAFP[2] unpubl. data
28 Sept. 1971	Delaware Point, Del.	72	3.5	22.0	4.9 m trawl	1	—	IA, Inc., Middletown
20 June 1972	Artificial Island, N.J.	79	3.0	22.0	4.9 m trawl	1	—	IA, Inc., Middletown
24 Sept. 1973	Newbold Island, N.J.	203	—	—	4.9 m trawl	1	196	IA, Inc., Middletown
Mar.-Dec. 1974	Burlington Island, N.J.	190	—	—	Cooling water intake	1	—	DRBAFP unpubl. data
23 May	Artificial Island	79	1.0	20.1	4.9 m trawl	1	340	IA, Inc., Middletown
Aug.	Bordentown, N.J.	206	—	—	4.9 m trawl	2	—	DRBAFP unpubl. data
8 May 1975	Artificial Island	79	5.0	17.5	14 cm gill net	1	700	IA, Inc., Middletown
19 May	Artificial Island	82	1.5	19.0	8 cm gill net	1	—	IA, Inc., Middletown
10-11 June	Newbold Island, N.J.	200	—	—	4.9 m trawl	1	[3]349	Martin Marietta Corp., 1976
Oct.-Dec.	Delaware Power Plant	163	—	—	Cooling water intake	1	—	DRBAFP unpubl. data
24 Mar. 1976	Artificial Island	79	0	8.6	8 cm gill net	1	765	IA, Inc., Middletown
10 May	Fishing Creek, N.J.	75	5.0	16.0	14 cm gill net	1	550	IA, Inc., Middletown
17 Mar. 1977	Little River	45	—	—	Gill net	1	1,117	Dovel 1979
4 Apr.	Appoquinimink River, Del.	82	—	—	4.9 m trawl	1	591	IA, Inc., Middletown
13 Apr.	Little River	45	—	—	Gill net	1	457	Dovel 1979
12 May	Artificial Island	86	5.0	16.0	4.9 m trawl	1	519	IA, Inc., Middletown
June	Pea Patch Island, Del.	98	—	—	Gill net	1	—	DRBAFP unpubl. data
27 June	Artificial Island	82	7.0	24.2	8 cm gill net	1	720	IA, Inc., Middletown
21 July	Artificial Island	82	5.0	28.0	8 cm gill net	1	680	IA, Inc., Middletown
18 Mar. 1978	Bowers Beach, Del.	38	—	—	Gill net	1	—	Dovel 1979
22 Mar.	Little River	45	—	—	Gill net	2	—	Dovel 1979
23 Mar.	Bowers Beach	38	—	—	Gill net	1	—	Dovel 1979
27 Mar.	Little River	45	—	—	Gill net	1	—	Dovel 1979
30 Mar.	Fowler Beach, Del.	15	—	—	Gill net	1	—	Dovel 1979
3 Apr.	Little River	45	—	—	Gill net	1	—	Dovel 1979

TABLE 1.—Recorded captures of Atlantic sturgeon, *Acipenser oxyrhynchus*, in the Delaware River estuary, November 1958-July 1980.—*Continued.*

Date	Area	River km	Salinity ‰	Temp (°C)	Method of capture	No	Total length (mm)	Source
7 Apr	Little River	45	—	—	Gill net	1	—	Dovel 1979
8 Apr	Del Haven, N J	17	—	—	Gill net	1	—	Dovel 1979
15 Apr	Little River	45	—	—	Gill net	1	—	Dovel 1979
22 Apr	Cohansey River, N J	61	8 0	17 0	4 9 m trawl	1	760	IA, Inc , Middletown
29 Apr	Del Haven	17	—	—	Gill net	1	—	Dovel 1979
May	Little River	45	—	—	Gill net	2	—	Dovel 1979
3 May	Del Haven	17	—	—	Gill net	1	—	Dovel 1979
6 May	Delaware Bay	—	—	—	Gill net	2	—	Dovel 1979
10 July	Harbor of Refuge	3	—	—	Hook and line	1	1,524	Del Dep Fish and Wildl
24 July	Artificial Island	80	4 0	27 0	4 9 m trawl	1	604	IA, Inc , Middletown
24 July	Elsinboro Point, N J	92	4 0	27 5	4 9 m trawl	1	678	IA, Inc , Middletown
24 July	Artificial Island	82	7 0	27 6	4 9 m trawl	1	518	IA, Inc , Middletown
15 Aug	Burlington Island	190	—	—	4 9 m trawl	1	157	IA, Inc , Absecon, N J
17 Aug	NE of Harbor of Refuge	1	29 0	25 2	4 9 m trawl	1	2,000	IA, Inc , Middletown
24 Aug	Artificial Island	82	5 0	27 7	4 9 m trawl	1	690	IA, Inc., Middletown
28 Aug	Burlington Island	190	0	25 0	4 9 m trawl	1	175	IA, Inc , Absecon
6 Sept	Burlington Island	190	0	25 0	4 9 m trawl	1	175	IA, Inc , Absecon
20 Sept	Artificial Island	80	7 0	23 4	4 9 m trawl	1	648	IA, Inc., Middletown
16 Apr 1979	Old Bare Shoal, Del	17	—	—	9 1 m trawl	1	855	Smith 1980
16 Apr	Hope Creek, N J	78	—	—	14 cm gill net	1	760	Commercial fisherman
20 Apr	Hope Creek	78	—	—	14 cm gill net	1	890	Commercial fisherman
20 Apr	Kitts Hummock, Del	41	—	—	13 cm gill net	1	610	Commercial fisherman
22 Apr	Kitts Hummock	41	—	—	10-13 cm gill net	2	900, 1,030	Commercial fisherman
23 Apr	Kitts Hummock	41	—	—	13 cm gill net	2	830, 980	Commercial fisherman
24 Apr	Kitts Hummock	41	–	—	13 cm gill net	2	865, 880	Commercial fisherman
25 Apr	Port Mahon, Del.	47	—	—	10 cm gill net	1	584	Commercial fisherman
25 Apr	Kitts Hummock	41	—	—	13 cm gill net	1	660	Commercial fisherman
25 Apr	Hope Creek	78	—	—	14 cm gill net	1	914	Commercial fisherman
26 Apr	Port Mahon	47	—	—	13 cm gill net	1	570	Commercial fisherman
26 Apr	Kitts Hummock	41	—	—	13 cm gill net	1	685	Commercial fisherman
29 Apr	Port Mahon	47	—	—	13 cm gill net	1	1,067	Commercial fisherman
29 Apr	Port Mahon	47	—	—	13 cm gill net	1	580	Commercial fisherman
30 Apr	Kitts Hummock	41	—	—	13 cm gill net	2	711, 865	Commercial fisherman
1 May	Port Mahon	47	—	—	13 cm gill net	1	810	Commercial fisherman
2 May	Port Mahon	47	—	—	13 cm gill net	2	720, 940	Commercial fisherman
3 May	Port Mahon	47	—	—	13 cm gill net	1	890	Commercial fisherman
6 May	Port Mahon	47	—	—	13 cm gill net	1	880	Commercial fisherman
9 May	Port Mahon	47	—	—	13 cm gill net	1	810	Commercial fisherman
11 May	Port Mahon	47	—	—	13 cm gill net	1	914	Commercial fisherman
12 May	Port Mahon	47	—	—	13 cm gill net	1	965	Commercial fisherman
21 May	W of Joe Flogger Shoal	42	20.0	16.7	9 1 m trawl	1	860	Smith 1980
22 May	Offshore Smyrna River, Del	71	13.0	18 3	9 1 m trawl	2	935, 1,117	Smith 1980
22 May	Ship John Shoal	58	17 0	18 1	9 1 m trawl	1	955	Smith 1980
12 June	Hope Creek	77	—	—	Dead on surface	1	889	IA, Inc., Middletown
21 June	W of Joe Flogger Shoal	42	24.0	19 6	9.1 m trawl	1	960	Smith 1980
22 June	Ship John Shoal	58	16.0	20.8	9 1 m trawl	2	1,190, 750	Smith 1980
12 July	Smyrna River	71	12.0	24.8	4 9 m trawl	1	960	IA, Inc , Middletown
July	Ship John Shoal	58	17.0	25 2	9 1 m trawl	1	815	Smith 1980
9 Aug	N of Pea Patch Island	101	1.0	28 1	4 9 m trawl	1	128	IA, Inc , Middletown
25 Sept	Bowers-Pickering Beaches, Del	38-44	—	—	Gill net	1	1,090	Commercial fisherman
Sept	Ship John Shoal	58	18 0	22 7	9 1 m trawl	1	1,150	Smith 1980
22 Oct	Harbor of Refuge	3	—	13.2	4.9 m trawl	1	810	IA, Inc , Middletown
Oct	Fourteen Ft Bank, Del	34	25.0	14.7	9.1 m trawl	1	875	Smith 1980
1 Nov	Offshore Prime Hook Beach, Del.	7	27 0	11.3	9.1 m trawl	1	1,100	Smith 1980
2 Nov	Artificial Island	80	6.0	15.0	Cooling water intake	1	936	IA, Inc , Middletown
16 Feb 1980	Artificial Island	80	10 0	0 5	Cooling water intake	1	692	IA, Inc., Middletown
24 Mar	Pickering Beach, Del.	44	—	—	Gill net	1	760	Commercial fisherman
25 Mar.	Pickering Beach	44	—	—	Gill net	4	457, 457, 760, 1,066	Commercial fisherman
26 Mar.	Pickering Beach	44	—	—	Gill net	1	1,220	Commercial fisherman
29 Mar	Pickering Beach	44	—	—	Gill net	1	1,524	Commercial fisherman
8 Apr	Artificial Island	80	1.0	9 5	Cooling water intake	1	[3]750	IA, Inc., Middletown
22 Apr	Pickering Beach	44	—	—	Gill net	1	760	Commerical fisherman
May	Old Bare Shoal, Del.	17	27 0	15 6	9 1 m trawl	1	1,010	Del Dep Fish and Wildl.
6 May	Artificial Island	80	4 0	17.0	Cooling water intake	1	689	IA, Inc , Middletown
19 May	Blake Channel	40	18 0	17 5	4 9 m trawl	1	927	IA, Inc , Middletown
28 May	Artificial Island	80	7 0	21 0	Cooling water intake	1	942	IA, Inc , Middletown
24 June	Reedy Island Dike, Del	84	—	—	Dead on surface	1	620	IA, Inc , Middletown
10 July	Sunken Ship Cove, N J.	80	—	—	Dead on beach	1	1,010	IA, Inc , Middletown
16 July	Artificial Island	80	—	—	Cooling water intake	1	[3]637	IA, Inc , Middletown
17 July	Offshore Smyrna River	71	14 0	25.3	9 1 m trawl	1	1,035	Del Dep Fish and Wildl
24 July	Artificial Island	80	10 0	28 0	Cooling water intake	1	1,015	IA, Inc., Middletown
31 July	Artificial Island	80	8.0	28.0	4 9 m trawl (surface)	1	1,230	IA, Inc , Middletown

[1]Ichthyological Associates, Inc.
[2]Delaware River Basin Anadromous Fishery Project
[3]Converted from fork length.

Bay, 53 in the lower tidal river, and 9 in the upper tidal river. A total of 64 specimens were captured in commercially fished gill nets, most as a bycatch of operations for American shad, and weakfish, *Cynoscion regalis*. The remaining 66 specimens were taken incidental to various fishery and ecological investigations; 23 by 4.9 m bottom trawl, 17 by 9.1 m bottom trawl, 12 by experimental gill net, 9 at industrial cooling water intakes, 1 by 4.9 m surface trawl, 1 by hook and line, and 3 were dead on the water's surface or on shore.

In Delaware Bay Atlantic sturgeon were taken from March through November (Fig. 2). Catch was greatest during March through May (14-23/mo), low during July through August (1/mo), and increased somewhat during September through November (2 or 3). The spring peak was composed largely of specimens captured in 1979 and 1980 by the cooperating commercial gill netters who logged incidental Atlantic sturgeon captures while fishing shallow waters off of Kitts Hummock (river km 41) and Port Mahon (river km 47), Del., in 1979 and Pickering Beach (river km 44), Del., in 1980. Their records reflect 27 specimens taken during 20 April-14 May 1979 and 8 during 24 March-22 April 1980. Additionally, all 18 Atlantic sturgeon reported from Delaware Bay by Dovel (1979) were taken during March-May (see Table 1). Although this abundance pattern may be biased by the greater fishing effort expended during spring relative to other seasons, essentially all other commercial gill netters interviewed reported the highest frequency of incidental sturgeon capture during spring. Most Atlantic sturgeon taken in the gill net fishery are apparently below marketable size and are released. Records indicate that survival in gill nets was very high if the nets were tended daily.

In the lower tidal river Atlantic sturgeon were taken from February through September and in December (Fig. 2); most during July (16), although moderate numbers (6-10) were taken from April through August. Eleven specimens were taken in late July and early August 1968, by two part-time commercial gill netters purposely fishing for Atlantic sturgeon. These men fished, typically for a 2-wk period in summer, between Delaware City (river km 98) and Liston Point (river km 77), Del., during the late 1940's through the early 1970's. They employed essentially traditional methods, as described by Cobb (1900), and drifted 9 × 572 m, 28 cm cotton mesh

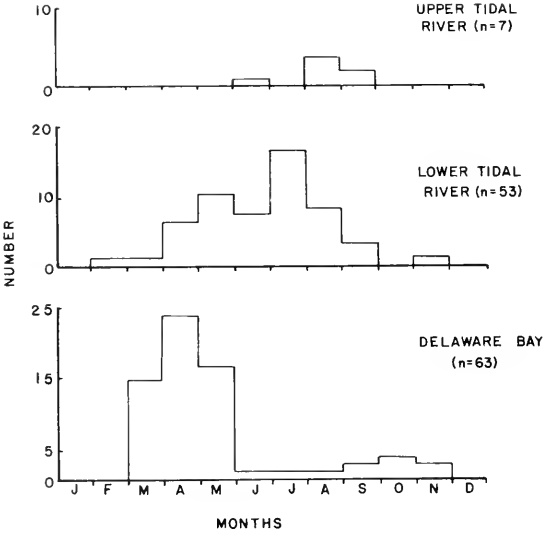

FIGURE 2.—Number of Atlantic sturgeon captured monthly in three regions of the Delaware River estuary, 1958-80.

gill nets along the bottom from about 1 h before to about 1 h after low tide (Beck[2]). These were, to the best of our knowledge, the last successful commercial efforts directed specifically at Atlantic sturgeon. Although the above mentioned 11 specimens are the only quantitative accounting of their catch available, anecdotal accounts indicate considerable success with as many as 191 specimens taken in a 2-wk period (Beck 1973).

In the upper tidal river, Atlantic sturgeon were captured in June (1), August (4), and September (2) (Fig. 2). Only one specimen was taken in the Wilmington, Del., to Philadelphia, Pa. (river km 114-170), reach. In this region mean dissolved oxygen concentrations approach zero during summer and are typically below 5 ppm during May through October (Freidersdorff et al. 1978). This fish was taken sometime during October-December 1975, when oxygen concentration was considerably higher.

Available data showed that Atlantic sturgeon occurred over a wide range of water temperature (0.5°-28.1°C) and salinity (0.0-29.0 ‰). The varying availability of temperature and salinity data by region, however, precludes further discussion. Values were available for 62% of the specimens captured in the lower tidal river but

[2]Robert A. Beck, Department of Natural Resources and Environmental Control Division of Fish and Wildlife, P.O. Box 1401, Dover, DE 19901, pers. commun. December 1978.

only 10% of those from Delaware Bay and 22% of those taken in the upper tidal river.

Length data were available for 97 Atlantic sturgeon. Reported fork length (FL) for 11 specimens were converted to total length (TL) with the relationship FL = 0.878 TL − 6.551, $r = 0.999$, calculated from measurements of 19 specimens. Total length ranged from 457 to 2,000 mm ($\bar{X}$ = 885 mm; $n = 45$) for specimens taken in Delaware Bay, from 128 to 1,431 mm ($\bar{X}$ = 863 mm; $n = 48$) in the lower tidal river, and from 157 to 196 mm ($\bar{X}$ = 176 mm; $n = 4$) in the upper tidal river (Fig. 3). Based on age-length data for the Hudson River estuary (Dovel 1979), the probable age of specimens taken in Delaware Bay ranged from 0+ to ca. 20+ and from 0+ to ca. 14+ in the lower tidal river. Only age 0+ specimens were taken in the upper tidal river. No individuals in spawning condition were reported.

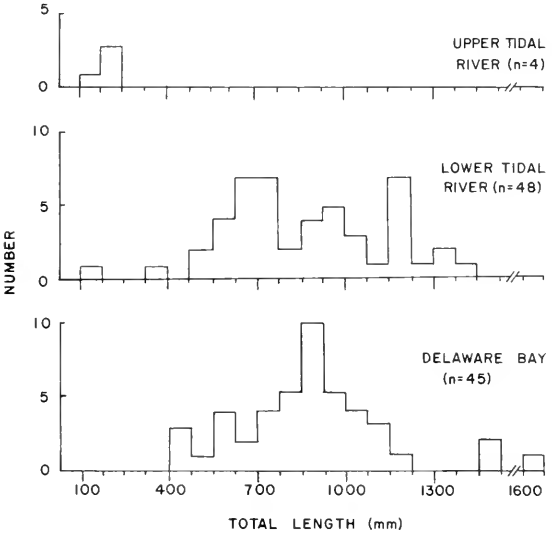

FIGURE 3.—Length-frequency distributions of Atlantic sturgeon captured in three regions of the Delaware River estuary, 1958-80.

DISCUSSION

Despite the limitations imposed by reliance on incidental catch records, a number of generalizations regarding the Atlantic sturgeon in the Delaware River estuary can be made. The data strongly indicate that there is a viable population of Atlantic sturgeon in the Delaware system which utilizes different regions of the estuary to varying degrees depending on season and life stage. A definite pattern of seasonal movement within the estuary can be inferred. In early spring substantial numbers of juvenile Atlantic sturgeon occurred in the shallow waters of Delware Bay; later in spring, abundance increased in the lower tidal river and this upstream movement continued through early summer. This is similar to the pattern described by Dovel (1979) for the Hudson River, i.e., juvenile Atlantic sturgeon overwinter in the deeper waters of the lower estuary and move upstream and inshore in spring in response to increasing water temperature. However, in the Delaware River estuary, juvenile Atlantic sturgeon ranged to the the fall line at Trenton, whereas in the Hudson River they were found only to river km 145 (Kingston, N.Y.), some 100 km below the limit of tidal intrusion.

During summer, Atlantic sturgeon were most abundant in the lower tidal portion of the Delaware River and probably use this region as a foraging ground. Numbers in this reach decreased somewhat during August, the month of maximum water temperature. Dovel (1979) reported that Hudson River Atlantic sturgeon seek cooler waters during summer and may move south before water temperature peaks. In the present study, however, no such movement to Delaware Bay during August was evident, although numbers in the bay increased slightly in September.

Abundance in the Delaware system decreased in the upper and lower tidal river in September and increased somewhat in Delaware Bay during September through November, suggesting a return to overwintering areas. Some individuals may have left the estuary at that time to overwinter in the nearshore ocean. Interviews conducted in 1978 and 1979 with commercial trawl fishermen operating out of Ocean City, Md., indicate that Atlantic sturgeon are commonly taken near the mouth of Delaware Bay in fall. Most of these fish are small, ranging from 0.6 to 1.5 m long, with occasional captures of larger individuals of 2.5-3.5 m.

Evidence on occurrence of older juveniles in the Delaware system disagrees with reports from other systems. Murawski and Pacheco (1977) reported that these fish emigrate from the estuary when they reach 760-915 mm long and do not return for a number of years until mature. Dovel (1979) found that Atlantic sturgeon between about 800 mm (ca. age 5) and 1,300 mm TL (ca. age 12) were rare in the Hudson River estuary and inferred that these individuals re-

mained at sea. However, in the Delaware River estuary Atlantic sturgeon between 800 and 1,300 mm were common and composed 62% of the measured specimens from Delaware Bay and 48% of those from the lower tidal river. It is possible that the Delaware River estuary is utilized during a greater portion of the Atlantic sturgeon's life cycle then is the Hudson. This may be associated with the relatively unimpacted condition of Delaware Bay and the lower Delaware River as compared with the heavily industrialized and degraded lower Hudson River estuary. It is also possible that an Atlantic sturgeon which has left the Hudson River may utilize other estuaries, including the Delaware system, during this portion of its life. Recapture of tagged Hudson River sturgeon in the Delaware River and more distant estuaries (Dovel 1979) may substantiate this view.

No specimens in spawning condition were recorded from the Delware River Estuary; most reported were probably immature. Most Atlantic sturgeon captured in the Delaware River estuary were <112 cm TL minimum for mature males and <200 cm for mature females reported by Dovel (1979). Larger mature specimens are almost certainly present in the estuary but are not vulnerable to the small-mesh gear typically fished by commercial fishermen and fishery biologists. Even though spawning location could not be ascertained it is perhaps signficant that the smallest specimen recorded (128 mm) was taken near Pea Patch Island, Del. (river km 101), an area historically described (Borodin 1925) as a principal spawning area for Atlantic sturgeon.

This compilation of incidental catches and a substantial body of anecdotal information suggests that Atlantic sturgeon may be far more abundant in the Delaware River estuary than commercial catch statistics and the impressions of other fishery scientists indicate (Hoff[3]). The reported scarcity of Atlantic sturgeon may be more the result of not fishing the appropriate gear in the right locations at the right times or of not monitoring fishermen who are. A more definitive status evaluation will require quantitative investigation to determine population size, mortality rate, age-specific fecundity, age at first reproduction, and spawning time and location. In any event, the value of incidental capture records and anecdotal accounts should be recognized and continued monitoring of available sources is advisable. The potential for restoration of the stock is high, based on the lack of industrial development in the lower estuary and the fact that as yet undammed, the Delaware River still features relatively natural run-off and river flow patterns. Pollution abatement programs, particularly those involved with improvement of dissolved oxygen levels in the Chester to Philadelphia reach will undoubtedly enhance this potential.

[3]James G. Hoff, Biology Department, Southern Massachusetts University, North Dartmouth, MA 02747, pers. commun. July 1980. See also, Hoff, J. G. 1980. Review of present status of the stocks of the Atlantic sturgeon, *Acipenser oxyrhynchus* (Mitchill). Southeastern Massachusetts Univ., North Dartmouth, 136 p.

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LARVAL DEVELOPMENT OF LABORATORY-REARED ROSYLIP SCULPIN, *ASCELICHTHYS RHODORUS* (COTTIDAE)

ANN C. MATARESE[1] AND JEFFREY B. MARLIAVE[2]

ABSTRACT

Larvae which hatched from egg masses collected at southwest Vancouver Island, Canada, were identified as *Ascelichthys rhodorus* and were successfully reared through transformation. A developmental series from yolk-sac larvae through newly settled juveniles (5.9-17.6 mm SL) is described and illustrated. Larvae hatch at approximately 6.0 mm SL and the yolk is absorbed by 6.5 mm SL. Notochord flexion begins between approximately 8.8 and 9.0 mm SL and is usually completed by 11.0 mm SL. Transformation to the juvenile stage begins between 12.0 and 13.0 mm SL and is complete in most of our larger specimens (15.0-16.0 mm SL).

Ascelichthys rhodorus larvae possess the following distinguishing characters: 1) pigment patterns along the ventral body and gut, 2) a pointed snout and moderately slender body as compared to other cottids, and 3) four prominent preopercular spines. A series of larvae is examined for meristic structures, including fin ray, vertebral and caudal development, and sequence of bone ossification. All structures except the caudal complex are ossified in our largest specimen (17.6 mm SL). Head and preopercular spination is discussed.

Minimum egg incubation time was 24 days (10°C); the minimum spawning period was 25 days. Larvae were examined for swimming behavior; older larvae maintained a relatively high speed schooling behavior throughout the planktonic phase. Settlement of juveniles started at 55-60 days, with ambivalence over reentry to the plankton until about 90 days, when settlement became permanent.

The rosylip sculpin, *Ascelichthys rhodorus*, is a small (11-15 cm) intertidal and subtidal cottid species distinguished by smooth skin, a low spinous dorsal fin, the absence of pelvic fins, and a single hooked preopercular spine (Hart 1973). Little is known of its biology and development or its relationships within the family Cottidae (Howe and Richardson 1978[3]). The geographic range of *A. rhodorus* extends from Moss Beach, Calif., northward to Sitka, Alaska (Miller and Lea 1972), and localized populations are commonly found throughout this range (Howe and Richardson footnote 3).

We provide here the first published description of the larvae of *A. rhodorus* with notes on the development and behavior of the species in the aquarium environment.

MATERIALS AND METHODS

Egg Collection and Laboratory Rearing

On 23 March 1979, nine unidentified egg masses were collected from under boulders on a cobble beach, at the 0.9 m tide level, at Jordan River (southwest Vancouver Island, Canada; lat. 48°25′20″N, long. 124°03′30″W). The egg masses were incubated in flowing seawater of about 10°C and 27‰ salinity at the Vancouver Public Aquarium. Only three tanks were available for rearing larvae, so some larvae that hatched on different dates were mixed. Rearing tanks were of 1,000 l volume, with inflow rates of over 1 tank volume/day. Newly hatched *Artemia salina* nauplii were fed in excess numbers to larvae once daily. Larvae were killed and preserved (3% Formalin[4] with sodium borate buffered seawater of 15‰ salinity) at weekly intervals until settlement from the planktonic stage started at 55-60 d. All preserved specimens were from two rearing tanks, one with a single sibling group and the other with a mixture of larvae from two separate hatching dates (Table 1). Surviving

[1]Northwest and Alaska Fisheries Center Seattle Laboratory, National Marine Fisheries Service, NOAA, 2725 Montlake Boulevard East, Seattle, WA 98112.

[2]Vancouver Public Aquarium, P.O. Box 3232, Vancouver, B.C. V68 3X8 Canada.

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

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

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TABLE 1.—Age and sibling relationships for *Ascelichthys rhodorus* larvae used for descriptions.

Tank	Date killed (1979)	Age (days)	Relationship[1]
1	26 Mar	3	1
1	9 Apr	14/17	2
1	13 Apr	18/21	2
Not reared	17 Apr	<1	—
2	17 Apr	8	1
1	17 Apr	22/25	2
1	26 Apr	31/34	2
2	1 May	22	1
1	1 May	36/39	2
1	1 May	36/39	2
1	9 May	44/47	2
2	23 May	44	1
1	23 May	58/61	2

[1]1 = siblings, all one age, same source.
2 = 2 sibling groups, mixed age, different source.

juveniles from both tanks were reared to maturity at the Vancouver Public Aquarium.

Taxonomic Specimens

Measurements

The following measurements were made on 64 unstained larvae of *A. rhodorus* (5.9-15.8 mm SL) using an ocular micrometer in a stereomicroscope:

Standard length (SL)—Snout tip to notochord tip prior to development of caudal fin, then to posterior margin of hypural bones.
Head length (HL)—Snout tip to posterior margin of opercle.
Snout to anus length—Distance along body midline from snout tip to a vertical line through center of anal opening.
Body depth at pectoral—Vertical distance from dorsal to ventral body margin at pectoral fin base.

Meristic Structures

A total of 49 larvae was cleared and stained for observation of various meristic structures and sequence of bone ossification. The following size ranges inadvertently were not preserved and are not represented in our discussion: 9.5-10.0 mm SL and 11.5-12.5 mm SL. Bone terminology follows Richardson and Washington (1980).

Specimens were stained using alizarin red and alcian blue (Dingerkus and Uhler 1977). Structures were considered ossified even if only slightly stained with alizarin red. Counts on stained larvae were made of dorsal fin spines and rays, anal fin rays, left pectoral fin rays, caudal fin rays, branchiostegal rays, and abdominal and caudal vertebrae (including the terminal ural centrum). Counts of caudal fin rays in juvenile and adult *A. rhodorus* were made from radiographs of six specimens (46-101 mm SL) from the collections in the College of Fisheries, University of Washington, Seattle. Twenty adult specimens (57-99 mm SL) were also cleared and stained for examination of the caudal fin.

The problems and inconsistencies of head spination terminology in cottid larvae have been discussed by Richardson and Washington (1980). We follow their terminology by using names proposed for *Sebastes* spp. (Richardson and Laroche 1979). Head spines for *A. rhodorus* larvae were examined on cleared and stained specimens in order to determine the origin of the spines.

Illustrations of larvae were made with the aid of a camera lucida.

IDENTIFICATION OF *ASCELICHTHYS RHODORUS*

The eggs of *A. rhodorus* range from 1.7 to 2.0 mm in diameter. Larvae hatch at approximately 6.0 mm SL and the yolk is absorbed by 6.5 mm SL. Notochord flexion begins between approximately 8.8 and 9.0 mm SL and is usually complete by 11.0 mm SL. Transforming larvae (about 12.0-13.0 mm SL) were distinguished by a combination of characters including changes in pigmentation and ossification of fin rays. Our largest specimens (15.0-18.0 mm SL) were newly settled and exhibited increased juvenile pigmentation.

The work of Richardson (1981) attempts to organize the cottid genera from the northeast Pacific that have been divided into phenetic groupings based on larval characters. In the northeast Pacific, larvae of 25 of 40 genera are described and most of the genera can be placed in 6 groups. Several genera are ungrouped (e.g., *Enophrys*, *Gymnocanthus*, and *Myoxocephalus*).

The present study indicates that *Ascelichthys* is most similar to the genera of Richardson's Group 2 (*Paricelinus*, *Triglops*, *Icelus*, *Chitonotus*, and *Icelinus*) which all possess the following characters: 1) moderately slender body form; 2) pointed snout; and 3) four prominent preopercular spines. Most members of this group also have postanal ventral midline melanophores sometimes extending along the caudal fin base. Although Richardson considers Group 2 coher-

ent, some differences are found among the genera in degree of gut pigmentation, head spination, number and position of postanal ventral melanophores, and myomere counts.

In degree of gut pigmentation, *A. rhodorus* larvae have a moderate intensity of melanophores; the gut is not as dark as *Paricelinus* but is darker than *Chitonotus*. *Ascelichthys rhodorus* do not have as many head spines as some members of Group 2 (e.g., *Triglops* and *Paricelinus*), possessing only parietal and nuchal spines and lacking spines in regions of the postocular, posttemporal-supracleithrum, opercle, and cleithrum. There is much variation among Group 2 genera in the number of ventral melanophores ranging from none in some species of *Triglops* to over 40 in *Chitonotus* (Richardson and Washington 1980). Larvae of *A. rhodorus* are most similar to larvae of *Paricelinus* in ventral pigmentation by having approximately 20-30 melanophores in preflexion larvae and approximately 15-20 melanophores in postflexion larvae. Myomere counts may also be useful in distinguishing *A. rhodorus* larvae. Myomere counts for *A. rhodorus* are most similar to those reported for *Chitonotus* and *Icelinus* (<40). *Triglops*, *Icelus*, and *Paricelinus* have >40 myomeres (Howe and Richardson footnote 3).

The absence of pelvic fins in *A. rhodorus* does not distinguish the early larvae since in most cottids the pelvic fins are the last fins to develop. However, in larger postflexion specimens the lack of pelvic fins does help to distinguish the species.

DEVELOPMENT OF *ASCELICHTHYS RHODORUS*

Pigment Patterns

A total of 35 larvae was examined for changes in larval pigmentation (Fig. 1). The following discussion describes general trends in melanophore distribution.

In the head region, pigment on early preflexion larvae is usually scattered dorsally over the head and nape; posterior to the eye, heavy internal pigment occurs at the base of the brain (Fig. 1A). With development, pigment increases in the area of the head, snout, mouth, operculum, and internally around the brain (Fig. 1B-E). A distinct patch of melanophores occurs at the jaw angle, first appearing between 6.0 and 8.0 mm SL and then becoming less prominent as larvae begin to transform (>12.0 mm SL). After 6.0 mm SL, pigment appears on the underside of the mouth along the median cartilage between the dentaries and urohyal (Fig. 1C). In the abdominal region, early larvae have a distinctly pigmented gut with large, stellate melanophores covering most of the abdominal cavity (Fig. 1A-C). Melanophores are also present on the isthmus and pectoral fin base of early larvae (Fig. 1B, C). With development, the external pigment covering the gut becomes more internal than external with only a few melanophores visible on the overlying skin (Fig. 1D).

An average of about 15 melanophores ($N = 12$, range 11-22) line the ventral body midline in 0-8 d (6.1-7.9 mm SL) *A. rhodorus* larvae, beginning well posterior to the anus at about myomeres 11-15 (Fig. 1A-C). These ventral melanophores show much variation in size and spacing among individual specimens. In general, the spacing between melanophores decreases from anterior to posterior with the last few spots appearing close together. The size of melanophores does not follow any pattern although usually the first 2 or 3 anterior spots are larger than the posterior ones. In preflexion larvae between 22 and 36 d (8.8-9.5 mm SL), the ventral melanophores extend further forward beginning at about the fifth myomere posterior to the anus and increase in number to over 20 ($N = 11$, range 23-28). Melanophores in the anterior half of the ventral midline pigment (about the first 12 spots) are more widely spaced and occur in the area where the anal fin is forming. In larger postflexion larvae at 44 d (10.2 mm SL), 15-20 ($N = 25$, range 9-22) ventral midline melanophores are present with the pigment beginning just posterior to the anus (Fig. 1D, E). The anterior melanophores along the developing anal fin are larger and are becoming more diffuse as they extend into the fin. Transforming specimens have fewer ventral spots, usually about 10 ($N = 23$, range 8-13), with most of them more internal than external (Fig. 1F). In these specimens, melanophores posterior to the completely developed anal fin appear more or less as a single row whereas those along the anal fin are aligned in a double row. In the tail region posterior to the ventral midline row of melanophores a group of caudal melanophores occurs near the tail tip on the early larvae (Fig. 1A). As the caudal fin develops, these melanophores begin to align in the area where the hypural bones are forming and in some specimens may extend onto the caudal fin (Fig. 1B, D).

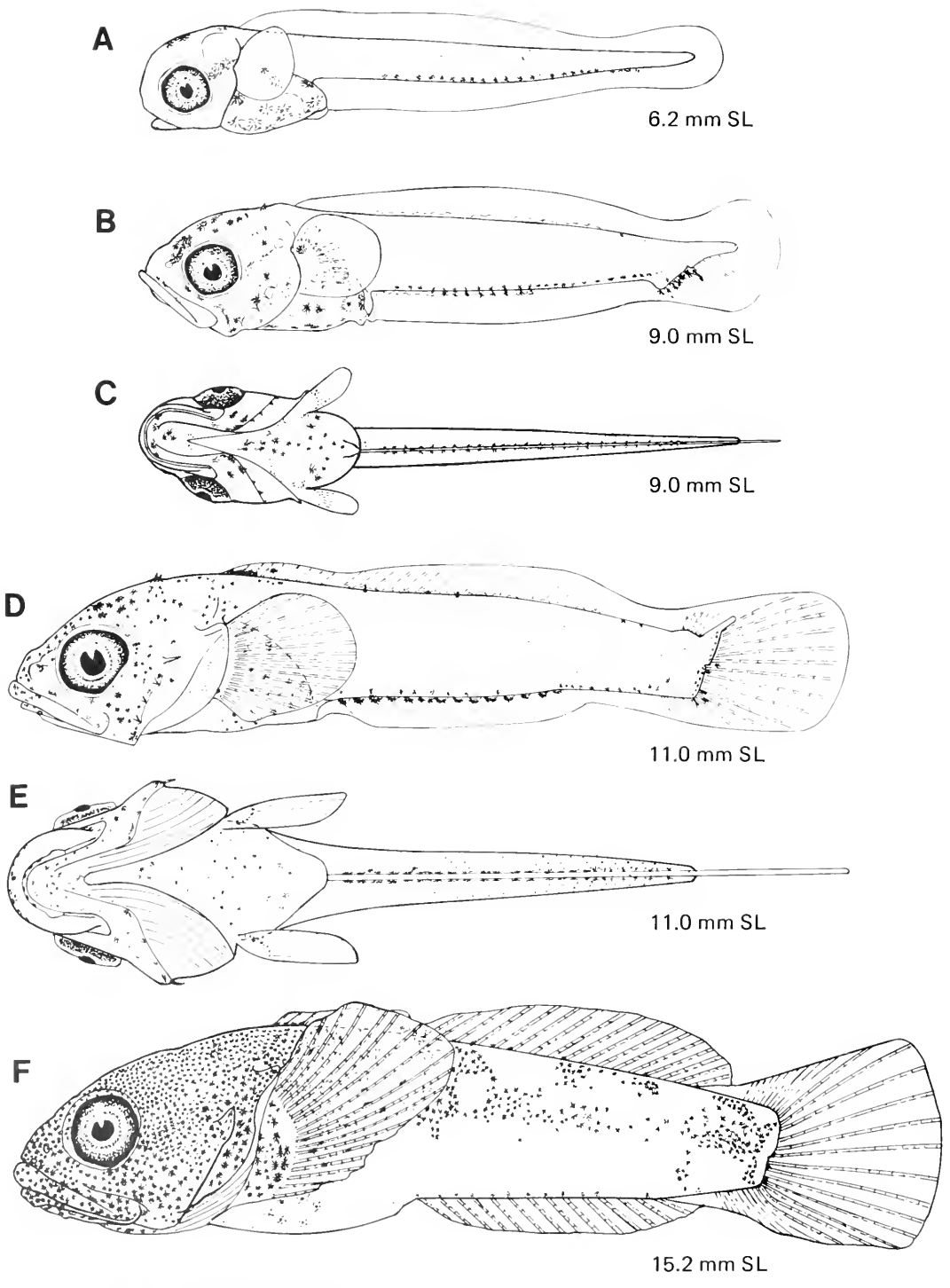


FIGURE 1.—Larval stages of *Ascelichthys rhodorus* showing changes in pigmentation: A. 6.2 mm SL; B. 9.0 mm SL; C. 9.0 mm SL (ventral view); D. 11.0 mm SL; E. 11.0 mm SL (ventral view); F. 15.2 mm SL.

Little pigment is added until the onset of transformation, except on the head, nape, and in the dorsal, anal, and caudal finfolds. Pigmentation changes occurring at the beginning of transformation are visible as early as 44 d after hatching (10.0-11.0 mm SL) but are not consistently visible until the 47th day (13.0 mm SL). During transformation *A. rhodorus* larvae show a rapid increase in pigmentation of all areas of the head and nape, and on the anterior dorsal body surface over the gut. A few melanophores appear in the dorsal portion of the postanal body becoming patches of pigment in the upper region dorsally and laterally (Fig. 1F). Melanophores also appear in the posterior caudal peduncle area. Early juveniles of the transformed, newly settled *A. rhodorus* have small, densely concentrated melanophores on the entire head, and several spots on the overlying skin over the gut cavity in addition to internal melanophores (Fig. 1F). The juveniles also have internal pigment along the notochord, and several distinctive groups of melanophore patches in the postanal body region along the upper body and in the caudal peduncle area. Dorsal body pigment on the largest specimens (17.0 mm SL) occurs in about five patches located under the posterior portion of the first dorsal fin, at the anterior, posterior, and center of the second dorsal fin, and in the posterior caudal area.

Morphology (Tables 2, 3)

Head length of *A. rhodorus* as a proportion of standard length increases with development and becomes almost one-third the standard length in early juveniles. Head length increases from 21.3% SL in preflexion larvae to 25.4% SL in larvae undergoing flexion. Values for head length continue to increase to 29.5% SL in postflexion larvae and 31.1% SL in transforming specimens. The head length of adult rosylip sculpin is slightly larger than our postflexion and transforming larvae; adult head lengths are generally about 37% SL (Hart 1973).

Eye diameter as a proportion of head length decreases with development. Preflexion larvae have diameters over half the size of the head (50.8% HL), decreasing to 36.6% HL in transforming larvae. Eye diameter continues to decrease in adult rosylip sculpin, usually measuring about 25% HL (Hart 1973).

Snout to anus length as a proportion of standard length increases with development. Snout length to anus length increases from one-third the standard length (33.2% SL) in preflexion larvae to 39.0% SL in larvae undergoing flexion.

TABLE 2.—Morphometries (in millimeters) of larvae and juveniles of *Ascelichthys rhodorus*. Approximate interval of notochord flexion is between dashed lines and interval of transformation is between solid lines.

Age[1] (days)	Standard length	Head length	Eye diameter	Snout to anus length	Body depth at pectoral
0	5.9	1.2	0.7	2.0	1.2
0	6.2	1.2	0.7	2.0	1.2
0	6.2	1.3	0.7	2.0	1.3
0	6.3	1.3	0.7	2.0	1.2
0	6.3	1.3	0.7	2.0	1.2
0	6.3	1.3	0.7	2.0	1.2
0	6.3	1.3	0.7	2.0	1.2
0	6.3	1.3	0.7	2.0	1.2
0	6.3	1.3	0.7	2.0	1.3
0	6.4	1.3	0.7	2.2	1.2
8	5.4	1.0	0.6	2.0	1.2
8	5.8	1.2	0.7	1.8	1.1
8	6.1	1.4	0.6	2.2	1.3
8	6.8	1.5	0.7	2.4	1.1
8	6.9	1.6	0.7	2.4	1.1
8	7.1	1.5	0.7	2.2	1.2
8	7.1	1.6	0.7	2.6	1.2
8	7.2	1.5	0.7	2.3	1.2
8	7.2	1.7	0.7	2.4	1.1
8	7.6	1.8	0.7	2.7	1.3
8	7.9	1.8	—	2.5	1.3
22	8.5	2.2	0.9	3.3	1.9
22	8.5	2.1	0.9	3.1	1.9
22	8.5	2.1	0.9	3.3	1.8
22	8.8	2.5	0.9	3.6	2.0
22	8.9	2.1	0.9	3.4	1.9
22	8.9	2.1	0.9	3.6	2.0
22	9.0	2.5	0.9	3.4	2.0
22	9.0	2.3	0.9	3.4	2.1
22	10.5	3.0	1.0	4.6	2.5
36/39	8.5	2.1	0.9	3.0	1.8
36/39	8.5	2.0	0.9	3.3	1.7
36/39	8.6	2.2	0.9	3.3	1.9
36/39	8.6	2.2	0.9	3.5	1.8
36/39	8.8	2.2	0.9	3.3	1.9
36/39	8.8	2.1	0.9	3.5	2.0
36/39	8.8	2.1	0.9	3.5	1.9
36/39	8.9	2.2	0.9	3.5	2.0
36/39	9.5	2.5	—	3.9	2.1
36/39	9.5	2.4	0.9	3.6	2.0
44	10.1	2.8	1.0	4.5	2.6
44	10.1	2.9	1.1	4.5	2.2
44	10.1	3.0	1.1	4.5	2.4
44	10.2	3.0	1.1	4.6	2.4
44	10.3	3.0	1.1	4.5	2.6
44	10.5	3.0	1.1	4.7	2.4
44	10.5	3.3	1.2	4.9	2.6
44	10.9	3.4	1.2	5.3	2.6
44	11.0	3.4	1.2	5.2	2.5
44	11.0	3.1	1.2	4.9	2.6
44/47	12.8	3.8	1.5	6.1	3.3
44/47	13.0	3.9	1.5	6.5	3.6
44/47	13.3	3.7	1.5	6.5	3.7
44/47	13.3	4.0	1.5	6.4	3.6
58/61	13.3	3.9	1.6	6.5	3.8
58/61	13.8	4.9	1.7	7.0	3.4
58/61	16.8	4.8	1.7	8.5	3.9
58/61	16.0	5.2	1.7	8.2	4.2
58/61	17.6	5.1	1.8	9.1	4.8
58/61	13.0	4.0	1.5	6.3	2.9
58/61	13.1	4.0	1.6	6.3	2.9
58/61	14.0	4.9	1.6	7.0	3.2
58/61	15.0	5.0	1.7	7.7	3.4
58/61	15.8	5.2	1.7	7.8	3.9

[1]Two ages separated by a slash indicates a mixed age group, different sibling groups (see Methods).

TABLE 3.—Body proportions of larvae and juveniles of *Ascelichthys rhodorus*. Values given for each body proportion are expressed as percent of standard length (SL) or head length (HL): mean, standard deviation, and range.

Body proportion	Preflexion	Flexion	Postflexion	Transforming
Sample size	21	19	10	14
Standard length (mm)	6.5±0.6 (5-8)	8.9±0.5 (8-11)	10.5±0.4 (10-11)	14.3±1.6 (13-18)
Head length/SL	21.3±1.4 (18-24)	25.4±1.6 (24-29)	29.5±1.3 (28-31)	31.1±2.4 (28-36)
Eye length/HL	50.8±6.4 (38-60)[1]	40.5±3.6 (30-45)[2]	36.6±1.1 (35-39)	36.6±3.0 (33-41)
Snout to anus/SL	33.2±2.0 (31-37)	39.0±2.0 (35-44)	45.4±1.6 (44-49)	49.6±1.3 (48-52)
Body depth at pectoral fin base/SL	18.5±1.9 (15-22)	22.0±0.9 (20-24)	23.8±1.2 (22-26)	25.2±2.3 (22-29)

[1]Sample size = 20.
[2]Sample size = 17.

Values for snout length to anus length continue to increase in postflexion larvae to 45.4% SL and to almost half the body length (49.6% SL) in transforming larvae.

Body depth at the pectoral fin base increases only slightly with development. Preflexion larvae have a body depth of 18.5% SL and values increase to 25.2% SL in transforming larvae. Adult body depths are usually about 28% SL (Hart 1973).

Meristic Structures (Table 4)

The following discussion of the development of meristic structures describes only general trends, as specimens show much variation in the sequence of bone ossification and our collection does not include all size ranges. Variation occurs frequently in the size of larvae with respect to the development of meristic structures. In general, the development of meristic characters appears dependent on size rather than age. Different growth rates as seen in standard length differences among individuals and between tanks are also reflected in the development of meristic structures (Tables 1, 4).

Oral Region

Branchiostegals are the first meristic structures to develop as ossification occurs as early as 6.8 mm SL. The full complement of six branchiostegals (seven in a few specimens) is not consistently ossified until the larvae are 9.0 mm SL.

Gill arches are stained blue by 9.0 mm SL and most begin to ossify between 8.8 and 9.5 mm SL. Ossification of gill rakers is complete by 13.3 mm SL.

Axial Skeleton

Abdominal and caudal centra begin to form between 8.8 and 9.0 mm SL, and development proceeds from anterior to posterior with the first signs of ossification occurring in larvae between 8.8 and 9.5 mm SL. Abdominal centra are completely ossified in 10.2 mm SL larvae. Caudal centra begin to ossify in 10.0 mm larvae and ossification of the completed vertebral column appears in 12.8 mm SL larvae.

Neural and haemal spines begin to ossify in larvae between 8.8 and 10.2 mm SL. All neural spines in the abdominal area are ossified by 10.2 mm SL, and the remaining neural spines in the caudal area are complete by 12.8-13.3 mm SL. Haemal spines took up red stain in our 10.2 mm SL larvae but are not completely ossified until 12.8-13.3 mm SL. Ossification of both neural and haemal spines proceeds anterior to posterior with the last neural and haemal spines associated with the caudal complex the last to ossify.

Fin Development

In general, all fins except caudal fin rays begin to ossify at 10.2 mm SL. Dorsal spines and pectoral fin rays are completely ossified by 12.8 mm SL, and dorsal and anal fin rays are fully ossified in 13.3 mm SL specimens.

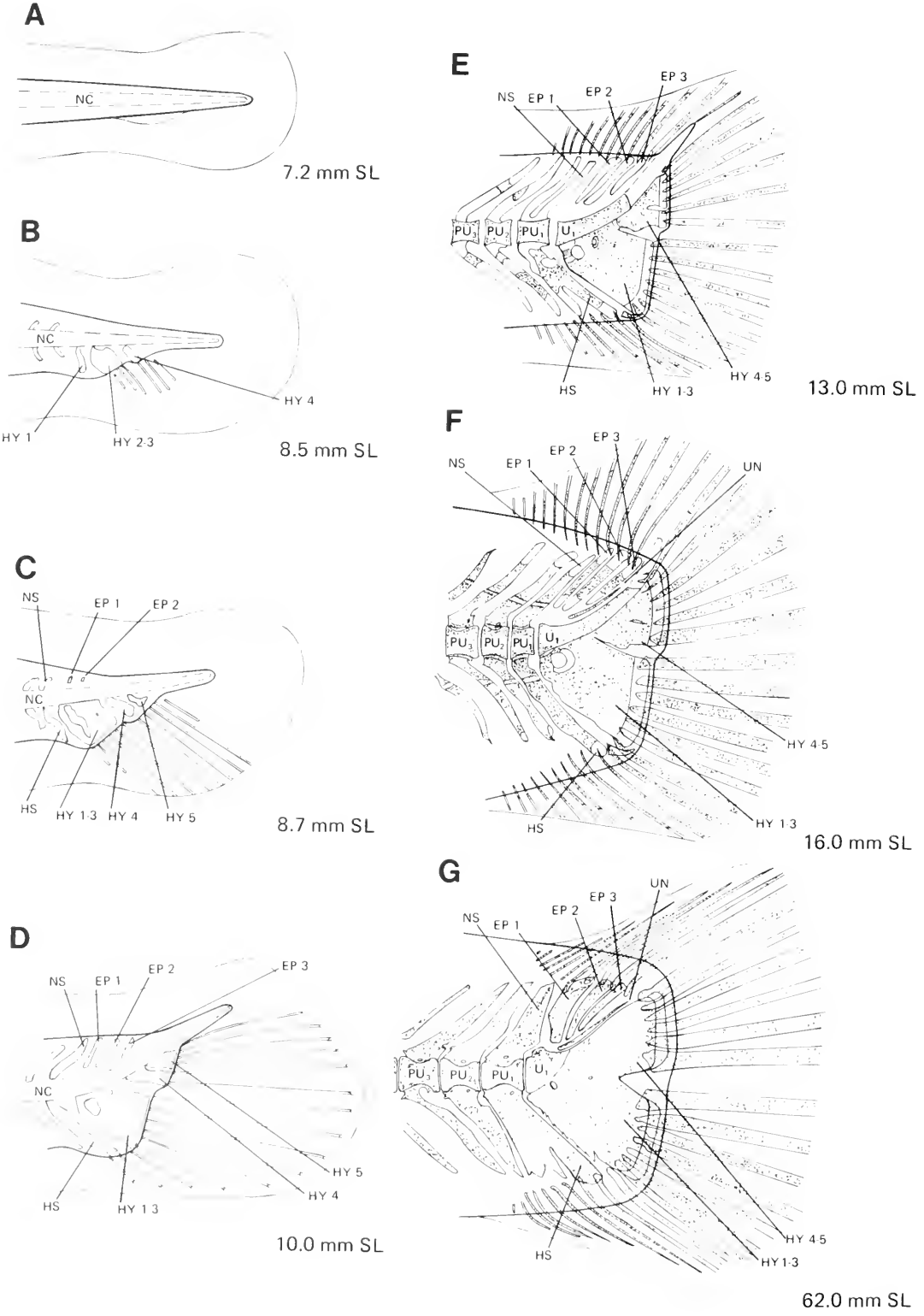
The caudal complex begins to ossify with the hypural bones in larvae between 12.8 and 13.3 mm SL. The following description is based on our available specimens although our largest juvenile (17.6 mm SL) does not have the full complement of ossified caudal fin rays.

The caudal fin is associated with a complex of 4-5 centra (1 ural and 3-4 preural centra), 3-4 neural and 3-4 haemal spines, 3 epurals, 1 superior hypural (HY 4-5), 1 inferior hypural (HY 1-3), and 1 pair of uroneurals (Fig. 2). Caudal fin rays total 31-37 of which 10-13 are superior secondary fin rays and 8-11 are inferior secondary fin rays. Principal caudal fin rays supported by the hypural bones number 13 (6 are supported by the

TABLE 4.—Meristic features of larval and early juvenile *Ascelichthys rhodorus*. Approximate interval of notochord flexion is between dashed lines and interval of transformation is between solid lines.

Standard length (mm)	Age[1] (days)	Fins						Vertebrae		Branchiostegals	Gills[2]	Head spines[3]					
		Dorsal		Anal rays	Pectoral rays	Caudal		Centra				Preopercular					
		Spines	Rays			Principal	Total	Abdominal	Caudal			1st	2d	3d	4th	Parietal	Nuchal
6.1	8											–	–	–	–	–	–
6.2	0											–	–	–	–	–	–
6.3	0											–	–	–	–	–	–
6.3	0											–	–	–	–	–	–
6.8	8									2		–	–	–	–	–	–
7.2	8											–	–	–	–	–	–
7.7	14/17									3							
7.9	8											–	–	–	–	–	–
7.9	14/17									2							
7.9	14/17									2							
8.0	22									6							
8.2	14/17									4							
8.4	14/17									2							
8.5	22									6							
8.7	14/17									4							
8.8	22									6		+	+	+	+	+	–
8.8	22									6		+	+	+	+	+	–
8.8	22							1		6		+	+	+	+	+	–
8.9	14/17									3							
9.0	22									6	X	+	+	+	+	+	–
9.0	22									6		+	+	+	+	+	–
9.5	22							2		6		+	+	+	+	+	–
9.5	22									6		+	+	+	+	+	–
10.0	31/34							9	2	6+7						+	–
10.0	31/34					3+3	6	11	5	6						+	–
10.2	36/39					3+3	6	9	4	6						+	+
10.2	36/39							11	4	7+7						+	
10.2	44	IX	19	16	16	4+4	8	11	11	6		+	+	+	+	+	–
10.2	44	IX	18	15	16	5+6	11	10	10	7+6		+	+	+	+	+	+
10.6	31/34					4+4	8	10	5	6						+	–
10.8	31/34					5+4	9	10	8	6						+	–
10.8	36/39					4+4	8	11	4	6						+	–
11.1	31/34					4+5	9	11	8	6						+	–
11.2	36/39					4+4	8	11	10	7+6						+	+
11.3	36/39					3+3	6	10	4	6						+	–
12.8	44/47	IX	13	13	18	6+7	20	10	24	6		+	+	+	+	+	+
13.3	44/47	IX	15	12	17	6+7	19	10	24	6	XX	+	+	+	+	+	+
13.3	58/61	IX	18	15	17	6+7	24	10	25	6		+	–	–	–	–	–
13.8	58/61	IX	19	14	17	6+7	29	10	25	6		+	–	–	–	–	–
16.8	58/61	IX	19	15	17	6+7	31	10	25	6+7		+	–	–	–	–	–
17.6	58/61	IX	18	14	17	6+7	39	10	25	6		+	–	–	–	–	–

[1]Two ages separated by a slash indicates a mixed age group, different sibling groups (see Methods).
[2]Gill rakers were not counted, X denotes onset of ossification of gill arches and XX denotes completed ossification of gill rakers.
[3]+ denotes spine present, – denotes spine absent.


A
NC
7.2 mm SL
B
NC
HY 4
HY 1
HY 2-3
8.5 mm SL
C
NS
EP 1
EP 2
NC
HS
HY 1-3
HY 4
HY 5
8.7 mm SL
D
NS
EP 1
EP 2
EP 3
NC
HY 5
HY 4
HS
HY 1-3
10.0 mm SL
E
NS
EP 1
EP 2
EP 3
PU3
PU2
PU1
U1
HS
HY 1-3
HY 4-5
13.0 mm SL
F
NS
EP 1
EP 2
EP 3
UN
PU3
PU2
PU1
U1
HY 4-5
HS
HY 1-3
16.0 mm SL
G
NS
EP 1
EP 2
EP 3
UN
PU3
PU2
PU1
U1
HS
HY 4-5
HY 1-3
62.0 mm SL

superior hypural and 7 are supported by the inferior hypural). Ahlstrom[5] generalized that all members of the family Cottidae probably have a total of 12 principal caudal rays, 6 supported by the superior hypural and 6 supported by the inferior hypural. Verification of this principal fin ray count came from counts on 20 adult specimens acquired for this study, 19 of which actually had a 6+7 count. Richardson[6] has also observed a number of exceptions to a 6+6 count in other members of the family Cottidae.

A symmetrical fin fold surrounds the tip of the notochord in newly hatched specimens 6.0 mm SL. In 7.2 mm SL larvae, a thickening is visible ventral to the notochord (Fig. 2A). By 8.5 mm SL, the ventral thickening is differentiated into three cartilaginous plates (Fig. 2B). The anterior plate represents hypural 1 (parhypural) followed by a larger plate presumably representing the fusion of hypurals 2 and 3. Posterior to hypurals 2 and 3, a third plate represents hypural 4. A few caudal fin rays are also visible by 8.5 mm SL. In slightly larger larvae of 8.7 mm SL the urostyle is just beginning to undergo notochord flexion, and the unossified hypural 1 has fused with hypurals 2 and 3 forming the inferior hypural plate (Fig. 2C). Also in 8.7 mm SL larvae, differentiation of hypural 5, and epurals 1 and 2 is visible (Fig. 2C). In larvae undergoing notochord flexion (10.0 mm SL) unossified hypurals 4 and 5 have begun fusing to form the superior hypural plate (Fig. 2D). We did not detect fusion of a sixth hypural bone during the formation of the superior hypural plate. If a sixth hypural bone develops late in the larval period as it does in the phylogenetically related blackgill rockfish, *Sebastes melanostomus*, (Moser and Ahlstrom 1978), it was not evident in the juveniles or adults we examined. The first appearance of unossifed epural 3 also occurs in specimens about 10.0 mm SL (Fig. 2D). Ossification proceeds rapidly once the larvae have undergone notochord flexion. By 13.0 mm SL, the ural centrum and all preural centra are ossified (Fig. 2E). The single ural centrum is not fused to the first preural centrum. Hypural bones, neural and haemal spines, and caudal fin rays have also begun ossifying in 13.0 mm SL specimens (Fig. 2E). By 16.0 mm SL, a completely ossified pair of uroneurals is visible dorsad to the urostyle (Fig. 2F). All three epurals have begun to ossify, thus completing the caudal complex except for a few unossified secondary caudal fin rays. This caudal complex of a 16.0 mm SL early juvenile resembles in all details that of a 62.0 mm SL adult (Fig. 2G). In a number of specimens abnormalities of the last neural and haemal spines were observed, e.g., double neural spines from the first preural centra (Fig. 2E) and a large flattened haemal spine (Fig. 2G).

Spination

Four similar-sized preopercular spines are ossified on specimens 8.8-9.0 mm SL (Fig. 1B). In 10.2 mm SL larvae the upper preopercular spine is larger than the lower three (Fig. 1D). After transformation the three lower spines are no longer visible, leaving only the prominent upper spine (Fig. 1F). The single hook shaped spine is visible on our largest specimens, appearing very similar to the single, recurved spine for which the adults are commonly known.

On specimens 8.8-9.0 mm SL, one small, parietal spine is evident (Fig. 1B). This spine remains prominent and is joined by a nuchal spine in 10.2 mm SL larvae (Fig. 1D). The parietal and nuchal spines are no longer visible in larvae >12.8 mm SL (Fig. 1F).

REPRODUCTIVE BEHAVIOR AND LARVAL REARING

Egg masses of *A. rhodorus* were found wedged in irregular spaces among rocks under larger boulders, but the eggs adhered only to other eggs, not to rock surfaces. No egg masses were found under boulders lying on sand, shell, gravel, or solid rock surfaces. The egg masses were taken only in a narrow band at the low water level, which was the lowest tidal level during March and early April 1979. This cobble beach had been repeatedly searched for fish eggs during lower tides before and after the period of the vernal equinox, i.e., in December, January, April, May, and June of previous years, but this kind of egg was only found during the moderate

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FIGURE 2.—Development of the caudal fin of *Ascelichthys rhodorus*: A. 7.2 mm SL; B. 8.5 mm SL; C. 8.7 mm SL; D. 10.0 mm SL; E. 13.0 mm SL; F. 16.0 mm SL; G. 62.0 mm SL. EP = epural; HS = haemal spine; HY = hypural; NC = notochord; NS = neural spine; PU = preural centrum; U = ural centrum; UR = uroneural. Ossified elements are stippled.

low tides of the vernal equinox. In April 1981, *A. rhodorus* eggs were found in the same area, but about half were dead while the remainder all hatched upon return to the laboratory. Perhaps the protracted exposure to air in April killed many of the earlier embryonic stages; an increase in embryonic temperature tolerance with development has been documented for another intertidal cottid, *Clinocottus acuticeps* (Marliave 1981a). Considering a relatively dense spawning of about one mass/3 m^2 found in March 1979, and the lack of egg masses at other times, this species might be characterized by a brief spawning season.

Superficially, *A. rhodorus* eggs resembled *Hexagrammos* spp. eggs in size (about 2.0 mm) and color, although there were far fewer eggs per mass. As with *Hexagrammos* spp., newly spawned eggs were a semitranslucent blue to purple, grading toward opaque white toward the egg center (personal observation by J. B. Marliave). Eggs with advanced embryos, showing guanine eye pigment, appeared brown overall, due to melanophores overlying dark olive yolk material. All egg masses were incubated and hatched in the laboratory; none were used for egg counts but some egg diameter measurements were taken. Hatching occurred on March 23 (1 mass) and 26 (1 mass) and on April 9 (3 masses) and 17 (4 masses). This range of hatching dates indicated a minimum spawning period of 25 d. The collection and final hatch dates indicated a minimum egg incubation period of 24 d at 10°C.

During the planktonic larval stage, larvae of *A. rhodorus* displayed relatively high-speed schooling behavior and a marked tendency toward startle responses. It is of note that both this species and another common northeastern Pacific Ocean fish, *Trichodon trichodon* (Marliave 1981b), are rare or unknown from plankton samples and school soon after hatching in the confines of a tank. Unlike *T. trichodon*, however, *A. rhodorus* larvae do not school immediately upon hatching but develop schooling behavior within 2 wk of hatching. *Ascelichthys rhodorus* larvae do not swim as fast as those of *T. trichodon*; *A. rhodorus* cruised at 2.5-7.5 body lengths/s at 2 wk of age, at 3-10 body lengths/s at 4 wk, and at 2.5-9.0 body lengths/s at 6 wk, with usual speeds close to 5 body lengths/s. From hatching onward, the *A. rhodorus* larvae were very easily disturbed, either by physical interference from other types of zooplankton, by movements of observers, or by abrupt changes in lighting. Startle responses were characterized by rapid bursts of undirected swimming which, in older larvae, effected the breakdown of schools.

After 2 wk, larval *A. rhodorus* schooled near the surface at all ages except for those larvae in tanks with larval shrimp, *Pandalus danae*. The *P. danae* occupied the surface layers and *A. rhodorus* schooled off the tank bottom until the *P. danae* settled from the plankton, after which *A. rhodorus* schooled near the surface. This pattern occurred successively in two separate tanks; no shrimp were present in the third tank. Thus, the vertical distribution of the *A. rhodorus* larvae was modified by the presence of other planktonic organisms.

Settlement to the bottom started at 55-60 d of age (14-18 mm SL) and schooling generally ceased. However, for unknown reasons all larvae in a tank would temporarily resume schooling from time to time. Between 60 and 90 d, there was a gradual increase in the proportion of settled larvae with no observed difference in feeding behavior between settled and schooling fish. By 90 d of age, the majority of juveniles were permanently settled and no further schooling was noted. Among cottids, protracted ambivalence about settlement from the plankton has been observed in *Gilbertidia sigalutes* (Marliave 1981c).

After initial settling was observed, substrate trays containing sand, gravel, and pebbles were placed in the tanks to determine substrate preferences of the larvae (Marliave 1977), but the trays were avoided. Larval *A. rhodorus* never settled against vertical surfaces, as is typical of a variety of other cottids which lack discreet substrate preferences (personal observation by J. B. Marliave). Settlement was typically on open bottom throughout the month of ambivalence between settlement and reentry to the plankton.

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A BEAK KEY FOR EIGHT EASTERN TROPICAL PACIFIC CEPHALOPOD SPECIES WITH RELATIONSHIPS BETWEEN THEIR BEAK DIMENSIONS AND SIZE

GARY A. WOLFF[1]

ABSTRACT

A method of identifying the beaks and estimating body weight and mantle length of eight common species of eastern tropical Pacific cephalopods is presented. Twenty specimens were selected from each of the following species: *Symplectoteuthis oualaniensis, Dosidicus gigas, Ommastrephes bartramii, Onychoteuthis banksii, Abraliopsis affinis, Pterygioteuthis giardi, Liocranchia reinhardti,* and *Loligo opalescens.* Seven dimensions measured on the upper beak and five dimensions measured on the lower beak are converted to ratios and compared individually among the species using an analysis of variance procedure and Tukey's ω. Significant differences ($\alpha \leq 0.05$) observed among the species' beak ratios means, in addition to structural characteristics, are used to construct artificial keys for the upper and lower beaks of the eight species. Upper and lower beak dimensions are used as independent variables in a linear regression model with mantle length and body weight (log transformed). Two equations are given for estimating the length and weight for each species from the upper or lower beak. One uses the rostral length dimension because of its durability and the second uses a dimension derived from a stepwise regression procedure.

The importance of cephalopods as prey is well documented for whales (Gaskin and Cawthorn 1967; Clarke et al. 1976; Clarke 1977), seals (Austin and Wilki 1950; Laws 1960), seabirds (Ashmole and Ashmole 1967; Imber 1978), tunas (Pinkas et al. 1971; Matthews et al. 1977), tunas and porpoise (Perrin et al. 1973), and sharks (Clarke and Stevens 1974; Tricas 1979). Due to the rapid digestion of the softer body parts, however, the cephalopod's beak is often the only identifiable structure remaining in these predator's stomachs as evidence of feeding on cephalopods. Consequently, the accuracy of specific identifications and estimates of cephalopod biomass consumed by these predators often suffers.

Two methods have generally been used to approach the problem of characterizing cephalopod beaks. A descriptive method was used most notably by Clarke (1962, 1980), Mangold and Fioroni (1966), and Pinkas et al. (1971). Families, genera, and occasionally species were identified from structural characteristics of the beak. A biometric method was used by Wolff (1977) and Wolff and Wormuth (1979) to separate two species of ommastrephid squid with beak dimensions. It was suggested that the method could be expanded to include other species of cephalopods.

This study presents a key based on structural and biometric differences among the beaks of eight species of cephalopods. The species of cephalopods examined were: *Symplectoteuthis oualaniensis* (Lesson), *Dosidicus gigas* (d'Orbigny), *Ommastrephes bartramii* (Lesueur), *Onychoteuthis banksii* (Leach), *Abraliopsis affinis* (Pfeffer), *Pterygioteuthis giardi* Fischer, *Liocranchia reinhardti* (Steenstrup), and *Loligo opalescens* Berry. Regression equations of body weight and mantle length from beak dimensions are also presented.

MATERIALS AND METHODS

The cephalopods for this study were obtained from Southwest Fisheries Center, National Marine Fisheries Service, and Invertebrate Collection, Scripps Institution of Oceanography, La Jolla, Calif. Twenty specimens of each species were selected in the maximum mantle length range available. Table 1 shows the ranges for mantle length and body weight and collection locations for the cephalopods. The buccal masses were removed, after the specimens were measured and weighed, and placed in a solution saturated with sodium borate and trypsin (8 g trypsin/l sodium borate solution) for 6 to 10 d.

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TABLE 1.—Mantle length (ML) ranges, body weight ranges, and collection locations for the species (nla = specimens collected in the Pacific but specific location not available).

Species	ML range (mm)	Weight range (g)	Number of specimens	Lat.	Long.
Symplectoteuthis oualaniensis	130-290	79-927	1	00°33′ S	111°14′ W
			2	03°25′ S	110°31′ W
			2	06°49′ S	86°14′ W
			1	05°12′ S	91°49′ W
			1	08°09′ S	100°31′ W
			1	05°46′ S	102°31′ W
			1	00°26′ S	109°28′ W
			1	01°15′ S	112°51′ W
			2	02°40′ S	116°11′ W
			1	00°01′ S	118°03′ W
			2	00°46′ S	105°35′ W
			1	02°52′ S	97°21′ W
			3	07°19′ S	94°24′ W
			1	05°14′ S	83°32′ W
Dosidicus gigas	196-321	191-842	2	00°33′ S	111°14′ W
			3	02°52′ S	97°21′ W
			3	07°49′ S	81°38′ W
			3	05°14′ S	83°32′ W
			1	01°46′ S	108°58′ W
			2	00°26′ S	109°28′ W
			1	06°49′ S	86°14′ W
			1	11°38′ S	87°13′ W
			1	06°00′ S	96°16′ W
			1	04°30′ S	89°16′ W
			1	11°30′ S	93°18′ W
			1	05°02′ S	91°49′ W
			1	02°52′ S	97°21′ W
			1	11°44′ S	83°56′ W
Ommastrephes bartramii	85-165	11-118	4	30°03′ N	156°11′ W
			2	30°08′ N	135°02′ W
			5	24°18′ N	155°00′ W
			9	28°11′ N	155°17′ W
Onychoteuthis banksii	40-130	3-67	2	13°00′ N	132°00′ W
			1	nla	
			1	25°10′ N	121°22′ W
			10	13°49′ N	118°59′ W
			3	18°00′ N	113°00′ W
			3	00°28′ N	105°53′ W
Abraliopsis affinis	19-26	0.5-4.3	5	24°06′ N	109°37′ W
			6	nla	
			7	11°31′ N	131°08′ W
			2	05°42′ N	86°53′ W
Pterygioteuthis giardi	16-30	0.3-1.4	1	05°02′ S	91°49′ W
			2	11°44′ S	83°56′ W
			2	10°24′ N	107°46′ W
			2	06°30′ N	139°00′ W
			2	00°04′ N	127°47′ W
			2	00°20′ N	120°21′ W
			9	01°21′ N	130°47′ W
Liocranchia reinhardti	23-125	1-24	1	00°30′ N	96°50′ W
			3	18°32′ N	119°51′ E
			1	32°34′ N	117°29′ W
			1	12°40′ N	112°46′ W
			14	13°49′ N	118°59′ W
Loligo opalescens	80-153	12-49	7	34°00′ N	120°10′ W
			6	26°30′ N	114°50′ W
			7	33°29′ N	117°47′ W

The beaks were then removed from the buccal masses and placed in 40% isopropyl alcohol.

Beak dimensions were measured with vernier calipers or an occular micrometer. Seven dimensions were measured on the upper beak of each specimen: length of the rostrum (RL), rostral tip to inner margin of wing (RW), length of hood (HL), width of the wing (WW), wing to crest length (WCL), jaw angle width (JW) and length of the crest (CL). Five dimensions were measured on the lower beak of each specimen: rostral tip to inner posterior corner of lateral wall (RC), rostral tip to inner margin of wing (RW), length of the rostrum (RL), length of the wing (WL), and jaw angle width (JW) (Fig. 1). These dimensions were transformed to ratios to remove the dimensionality. Comparisons among species' beak ratios were made with a one-way classification analysis of variance procedure (ANOVA). The ratios were normally distributed and the ratio

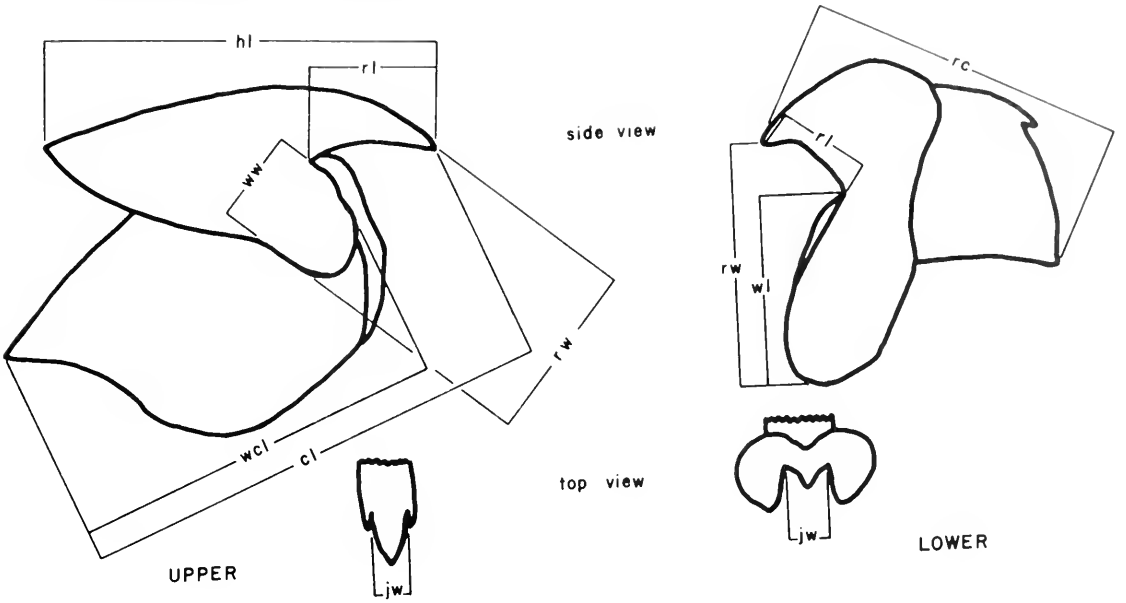


FIGURE 1.—Dimensions measured on the upper and lower beak.

transformation met the criteria for validity as described by Anderson and Lydic (1977). Tukey's ω procedure was used to test for significant differences ($\alpha \leq 0.05$) among 21 ratio means from the upper beak and 10 ratio means from the lower beak for each species. This procedure involves the computation of a confidence interval from the formula: $\omega = q_{\alpha}\ (p,\ n_2)\ s_{\bar{r}}$, where ω is a range for the treatment means with a given probability level ($\alpha \leq 0.05$), q is the studentized range, p is the number of treatments, n_2 is the error degrees of freedom and $s_{\bar{r}}$ is the standard error of the treatment means (Steel and Torrie 1960). Simple linear regressions were calculated to express the relationship between a beak dimension and the mantle length and log transformed body weight. An AMDAHL 470 V/6 computer[2] performed the majority of computations.

RESULTS

The results of the ANOVA procedure are summarized in Tables 2 and 3. The species' means are ranked and the standard error of the treatment mean for each ratio is given. These tables form the basis for the construction of the biometric portion of the beak key. Combinations of descriptive characteristics and significant beak ratios are used to identify the eight species of cephalopods. Separate keys are provided for the upper and lower beak.

The ratio values presented in the key are midpoints between species' means and often greatly exceed the stated significance level ($\alpha \leq 0.05$) as indicated by the confidence interval for the species' means which follows in parentheses. Additional descriptive characteristics and alternate beak ratios are given to corroborate the initial identification. Figures 3-10 show upper and lower beaks for each of the species. A few of the alternate ratios in the upper and lower beak key have species' means which are not significantly different. These ratios can be considered reliable since Hartley (1955) suggested that the experimentwise error rate could be relaxed considerably below the standard $\alpha \leq 0.05$ level due to the conservative nature of Tukey's ω procedure. Additional alternate ratio values can be determined from Table 2 to distinguish species if the ratios in the key are not satisfactory (e.g., damaged beak). The descriptive characteristics follow a slightly modified version of Clarke's terminology (1962, 1980) with several additions as shown in Figure 2. This key should be used with caution on specimens which are greatly outside the size range of this study.

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

TABLE 2.—Upper beak ratio means ($\bar{x}$) and standard error of the treatment means ($s_{\bar{x}}$) ($\omega = 4.3_{0.5}$ (8, 152) $s_{\bar{x}}$). So = *Symplectoteuthis oualaniensis*, Dg = *Dosidicus gigas*, Ob = *Ommastrephes bartramii*, Obnk = *Onychoteuthis banksii*, Aa = *Abraliopsis affinis*, Pg = *Pterygioteuthis giardi*, Lr = *Liocranchis reinhardti*, Lo = *Loligo opalescens*.

$s_{\bar{x}}$	Ratio	Species							
0.0130	RL/RW	So	Dg	Ob	Obnk	Aa	Pg	Lr	Lo
	$\bar{x}$	0.766	0.682	0.606	0.599	0.592	0.580	0.523	0.485
0.0051	RL/HL	So	Aa	Dg	Obnk	Pg	Ob	Lr	Lo
	$\bar{x}$	0.354	0.345	0.335	0.316	0.313	0.309	0.290	0.246
0.0351	RL/WH	So	Aa	Dg	Obnk	Pg	Ob	Lr	Lo
	$\bar{x}$	1.507	1.341	1.282	1.190	1.151	1.111	0.941	0.863
0.0058	RL/WCL	So	Dg	Ob	Aa	Pg	Obnk	Lr	Lo
	$\bar{x}$	0.358	0.354	0.319	0.306	0.287	0.287	0.261	0.211
0.0148	RL/JW	Obnk	So	Dg	Aa	Ob	Pg	Lr	Lo
	$\bar{x}$	1.349	1.215	1.161	1.128	1.061	1.042	0.963	0.936
0.0038	RL/CL	So	Dg	Ob	Aa	Pg	Obnk	Lr	Lo
	$\bar{x}$	0.288	0.280	0.252	0.234	0.226	0.218	0.211	0.177
0.0136	RW/HL	Aa	Lr	Pg	Obnk	Ob	Lo	Dg	So
	$\bar{x}$	0.585	0.557	0.542	0.528	0.510	0.509	0.491	0.463
0.0571	RW/WW	Aa	Obnk	Pg	So	Dg	Ob	Lr	Lo
	$\bar{x}$	2.254	1.980	1.979	1.968	1.878	1.831	1.799	1.757
0.0141	RW/WCL	Ob	Dg	Aa	Lr	Pg	So	Obnk	Lo
	$\bar{x}$	0.526	0.519	0.518	0.502	0.496	0.467	0.452	0.435
0.0532	RW/JW	Obnk	Lo	Aa	Lr	Pg	Ob	Dg	So
	$\bar{x}$	2.257	1.955	1.916	1.851	1.806	1.758	1.705	1.586
0.0190	RW/CL	Ob	Dg	Lr	Aa	Pg	So	Lo	Obnk
	$\bar{x}$	0.416	0.411	0.405	0.396	0.391	0.376	0.365	0.364
0.0751	HL/WW	So	Aa	Dg	Obnk	Pg	Ob	Lo	Lr
	$\bar{x}$	4.253	3.870	3.827	3.756	3.660	3.594	3.460	3.244
0.0095	HL/WCL	Dg	Ob	So	Pg	Lr	Aa	Obnk	Lo
	$\bar{x}$	1.058	1.033	1.010	0.917	0.901	0.884	0.856	0.855
0.0593	HL/JW	Obnk	Lo	Dg	Ob	So	Pg	Lr	Aa
	$\bar{x}$	4.277	3.846	3.474	3.453	3.431	3.332	3.324	3.279
0.0061	HL/CL	Dg	Ob	So	Lr	Pg	Lo	Obnk	Aa
	$\bar{x}$	0.837	0.817	0.813	0.728	0.722	0.718	0.689	0.677
0.0055	WW/WCL	Ob	Lr	Dg	Pg	Lo	So	Aa	Obnk
	$\bar{x}$	0.288	0.280	0.277	0.253	0.249	0.238	0.232	0.230
0.0309	WW/JW	Obnk	Lo	Lr	Ob	Pg	Dg	Aa	So
	$\bar{x}$	1.148	1.135	1.036	0.966	0.922	0.910	0.861	0.811
0.0045	WW/CL	Ob	Lr	Dg	Lo	Pg	So	Obnk	Aa
	$\bar{x}$	0.228	0.226	0.219	0.210	0.199	0.192	0.185	0.178
0.0785	WCL/JW	Obnk	Lo	Aa	Lr	Pg	So	Ob	Dg
	$\bar{x}$	5.014	4.516	3.719	3.693	3.642	3.399	3.342	3.284
0.0038	WCL/CL	Lo	Lr	So	Obnk	Dg	Ob	Pg	Aa
	$\bar{x}$	0.841	0.808	0.806	0.805	0.791	0.791	0.788	0.767
0.0033	JW/CL	Dg	Ob	So	Lr	Pg	Aa	Lo	Obnk
	$\bar{x}$	0.241	0.238	0.238	0.219	0.218	0.207	0.188	0.162

TABLE 3.—Lower beak ratio means ($\bar{x}$) and standard error of the treatment means ($s_{\bar{x}}$).

$s_{\bar{x}}$	Ratio	Species							
0.0138	RC/RW	Lo	Dg	Pg	Aa	Ob	So	Obnk	Lr
	$\bar{x}$	1.235	1.232	1.213	1.209	1.200	1.199	1.186	1.142
0.0509	RC/RL	Lo	Lr	Pg	Obnk	Ob	Aa	Dg	So
	$\bar{x}$	4.058	3.580	3.424	3.222	2.967	2.960	2.807	2.783
0.0221	RC/WL	Dg	So	Ob	Aa	Obnk	Pg	Lo	Lr
	$\bar{x}$	1.829	1.756	1.700	1.689	1.644	1.552	1.526	1.513
0.879	RC/JW	Lr	Lo	Aa	Ob	Pg	Dg	Obnk	So
	$\bar{x}$	4.402	4.025	3.852	3.673	3.525	3.357	3.341	2.996
0.0504	RW/RL	Lo	Lr	Pg	Obnk	Ob	Aa	So	Dg
	$\bar{x}$	3.289	3.139	2.828	2.722	2.475	2.459	2.323	2.280
0.0148	RW/WL	Dg	So	Ob	Aa	Obnk	Lr	Pg	Lo
	$\bar{x}$	1.485	1.465	1.418	1.398	1.387	1.327	1.280	1.236
0.0729	RW/JW	Lr	Lo	Aa	Ob	Pg	Obnk	Dg	So
	$\bar{x}$	3.867	3.258	3.179	3.066	2.918	2.822	2.727	2.500
0.0115	RL/WL	Dg	So	Ob	Aa	Obnk	Pg	Lr	Lo
	$\bar{x}$	0.653	0.632	0.577	0.575	0.512	0.457	0.425	0.380
0.0274	RL/JW	Aa	Ob	Lr	Dg	So	Obnk	Pg	Lo
	$\bar{x}$	1.308	1.243	1.235	1.197	1.077	1.037	1.032	0.996
0.0597	WL/JW	Lr	Lo	Pg	Aa	Ob	Obnk	Dg	So
	$\bar{x}$	2.911	2.641	2.296	2.284	2.168	2.039	1.838	1.709

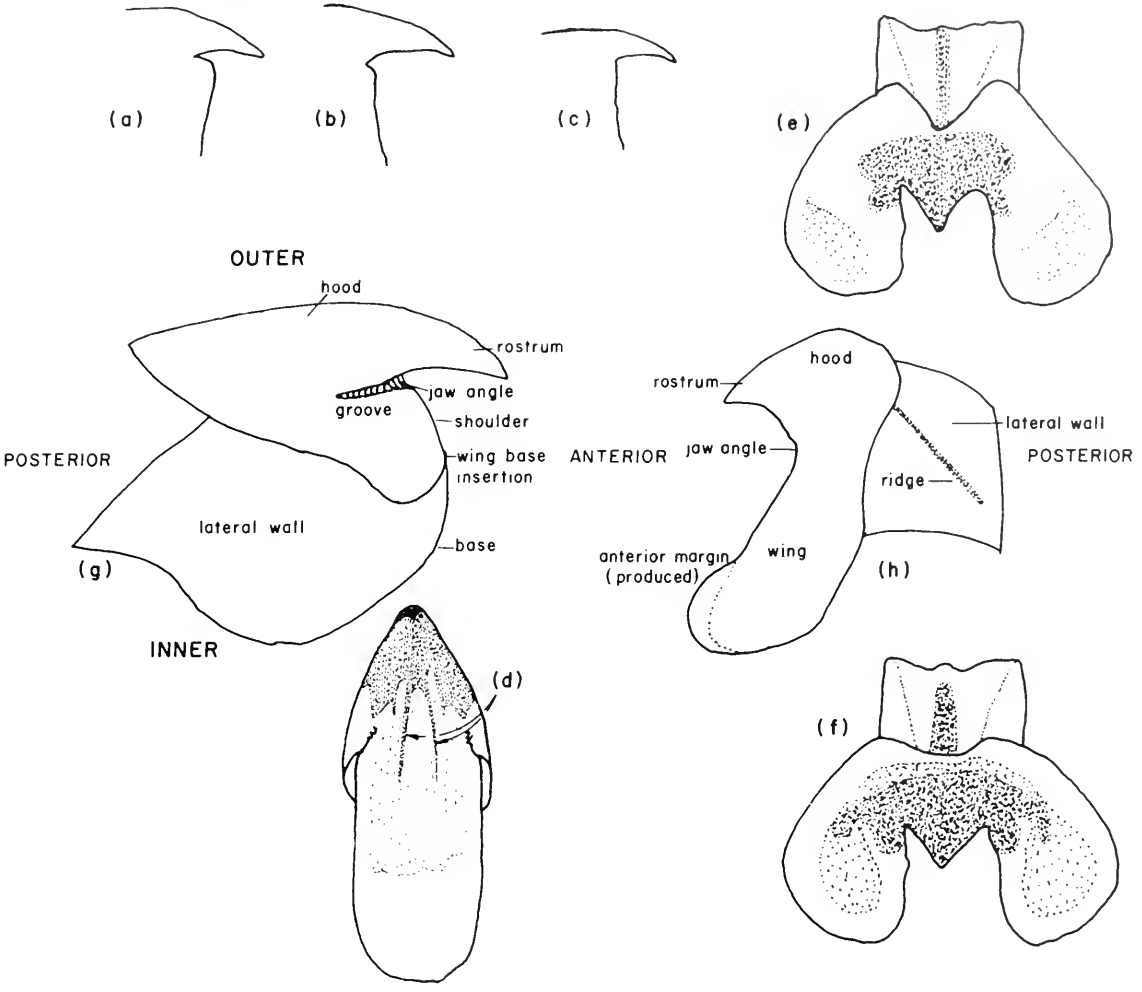


FIGURE 2.—Descriptive characteristics of the upper and lower beak; (a) deeply recessed jaw angle, (b) moderately recessed jaw angle, (c) jaw angle not recessed, (d) pigment stripes on inner surface of rostrum and crest, (e) hood deeply notched at crest, (f) hood slightly notched at crest, (g) upper beak characteristics, (h) lower beak characteristics.

KEY TO THE UPPER BEAK

*Alternate beak ratio
**Alternate beak ratio CI greater than the difference between the species means.

1a.	Jaw angle deeply recessed	6
1b.	Jaw angle not deeply recessed	2
2a.	Prominent groove at jaw angle	3
2b.	Groove absent at jaw angle	4

3a. RL/JW >1.24 (CI_{05} = 1.349±0.032); *HL/JW >3.78 (CI_{05} = 4.277±0.127); *RL/HL <0.33 (CI_{05} = 0.316±0.011) ..... *Onychoteuthis banksii*
Jaw angle slightly recessed; anterior-posterior groove at jaw angle ⅓ of RL (Fig. 2); wing base inserted ¾ down anterior margin of lateral wall; pigment changes with growth shown in Figure 3.

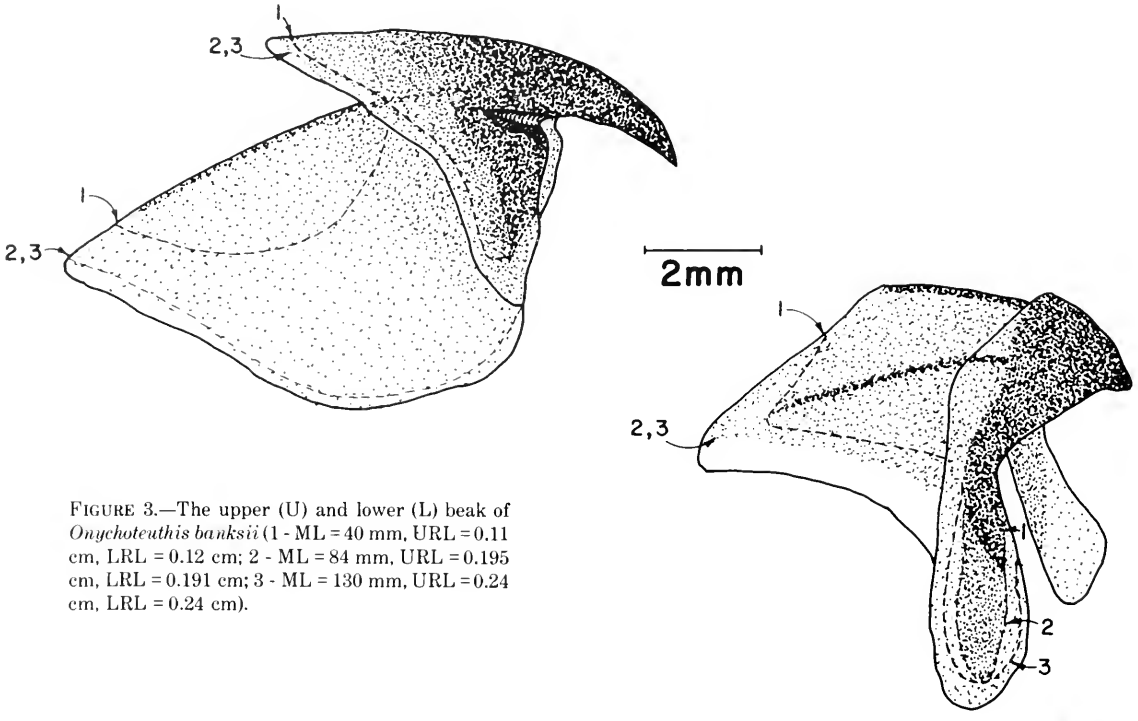
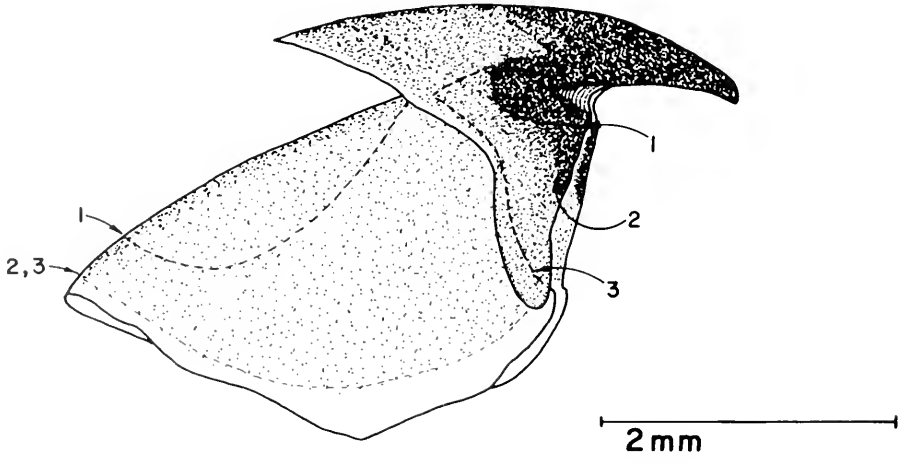


FIGURE 3.—The upper (U) and lower (L) beak of *Onychoteuthis banksii* (1 - ML = 40 mm, URL = 0.11 cm, LRL = 0.12 cm; 2 - ML = 84 mm, URL = 0.195 cm, LRL = 0.191 cm; 3 - ML = 130 mm, URL = 0.24 cm, LRL = 0.24 cm).

3b. RL/JW <1.24 (CI_{05} = 1.128±0.032); *HL/JW <3.78 (CI_{05} = 3.279±0.127); *RL/HL >0.33 (CI_{05} = 0.345±0.011) ..... *Abraliopsis affinis*
Jaw angle slightly recessed; anterior-posterior groove at jaw angle <¼ of RL (Fig. 2); wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 4.



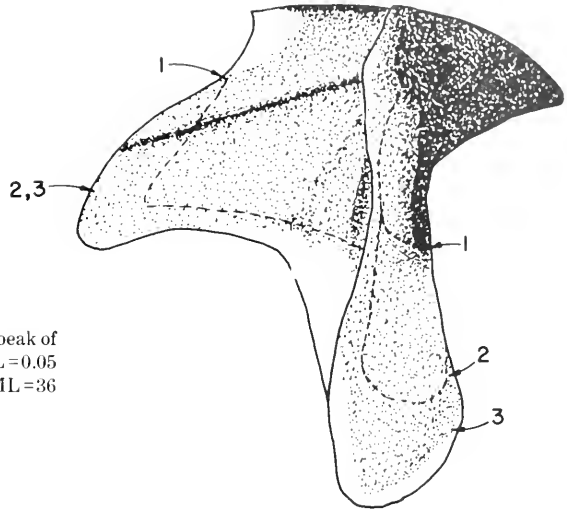
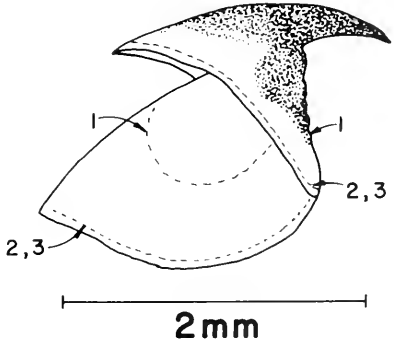


FIGURE 4.—The upper (see bottom of p. 362) and lower beak of *Abraliopsis affinis* (1 - ML = 19 mm, URL = 0.05 cm, LRL = 0.05 cm; 2 - ML = 32 mm, URL = 0.10 cm, LRL = 0.10 cm; 3 - ML = 36 mm, URL = 0.12 cm, LRL = 0.14 cm).

4a. RL/JW <1.003 (CI_{05} = 0.963±0.032) 5

4b. RL/JW >1.003 (CI_{05} = 1.043±0.032); *RL/HL >0.301 (CI_{05} = 0.313±0.011); *RL/CL >0.218 (CI_{05} = 0.226±0.008) ..... *Pterygioteuthis giardi*
Jaw angle not recessed; wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 5.



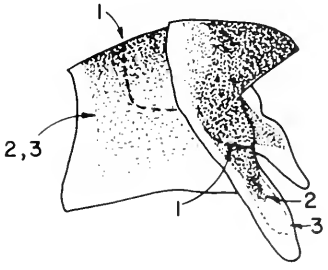


FIGURE 5.—The upper and lower beak of *Pterygioteuthis giardi* (1 - ML = 16 mm, URL = 0.03 cm, LRL = 0.03 cm; 2 - ML = 22 mm, URL = 0.05 cm, LRL = 0.05 cm; 3 - ML = 30 mm, URL = 0.06 cm, LRL = 0.05 cm).

5a. RL/HL >0.268 (CI_{05} = 0.290±0.011); *RL/CL >0.194 (CI_{05} = 0.211±0.008); *JW/CL >0.204 (CI_{05} = 0.219±0.007) ..... *Liocranchia reinhardti*
Jaw angle not recessed; wing base inserted 2/3 down anterior margin of lateral wall; pigment changes with growth shown in Figure 6.

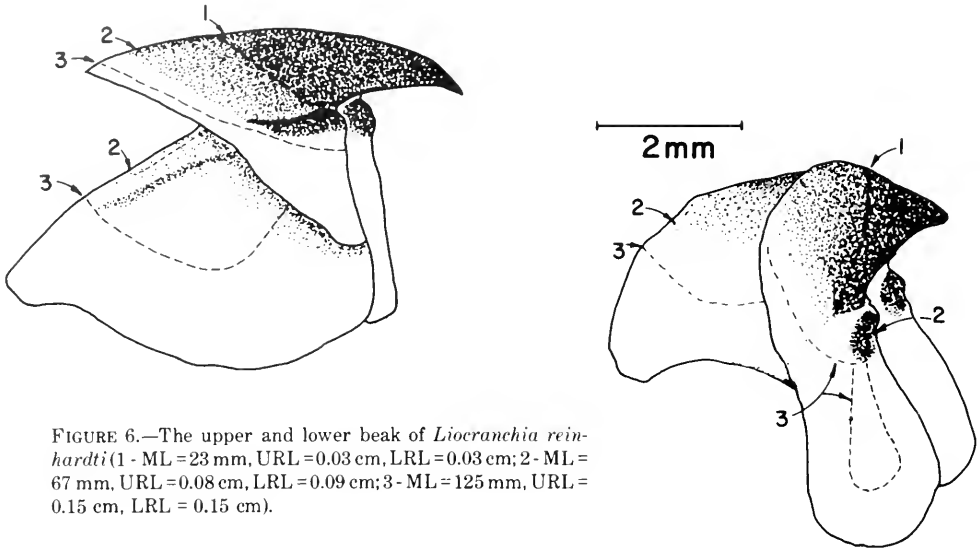


FIGURE 6.—The upper and lower beak of *Liocranchia reinhardti* (1 - ML = 23 mm, URL = 0.03 cm, LRL = 0.03 cm; 2 - ML = 67 mm, URL = 0.08 cm, LRL = 0.09 cm; 3 - ML = 125 mm, URL = 0.15 cm, LRL = 0.15 cm).

5b. RL/HL <0.268 (CI_{05} = 0.246±0.011); *RL/CL <0.194 (CI_{05} = 0.177±0.008); *JW/CL <0.204 (CI_{05} = 0.188±0.007) ..... *Loligo opalescens*
Jaw angle not recessed; wing base inserted just above base of anterior margin of lateral wall; pigment changes with growth shown in Figure 7.

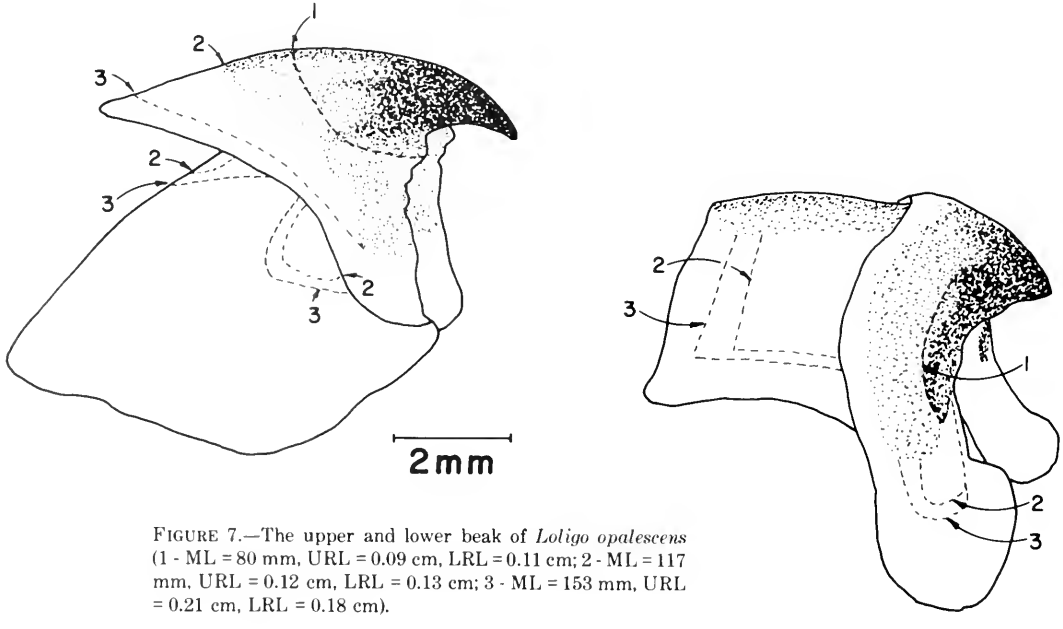


FIGURE 7.—The upper and lower beak of *Loligo opalescens* (1 - ML = 80 mm, URL = 0.09 cm, LRL = 0.11 cm; 2 - ML = 117 mm, URL = 0.12 cm, LRL = 0.13 cm; 3 - ML = 153 mm, URL = 0.21 cm, LRL = 0.18 cm).

6a. RL/JW >1.111 (CI_{05} = 1.161±0.032) 7

6b. RL/JW <1.111 (CI_{05} = 1.061±0.032); *RL/HL <0.322 (CI_{05} = 0.309±0.011); *RL/CL <0.266 (CI_{05} = 0.252±0.008) ..... *Ommastrephes bartramii*

Jaw angle deeply recessed; wing base inserted ⅔ down anterior margin of lateral wall; two pigment stripes present as in *Dosidicus gigas* (Fig. 2), remain in beaks with URL >0.60 cm; pigmentation in lateral wall is absent in beaks with URL <0.60 cm; other pigment changes with growth shown in Figure 8.

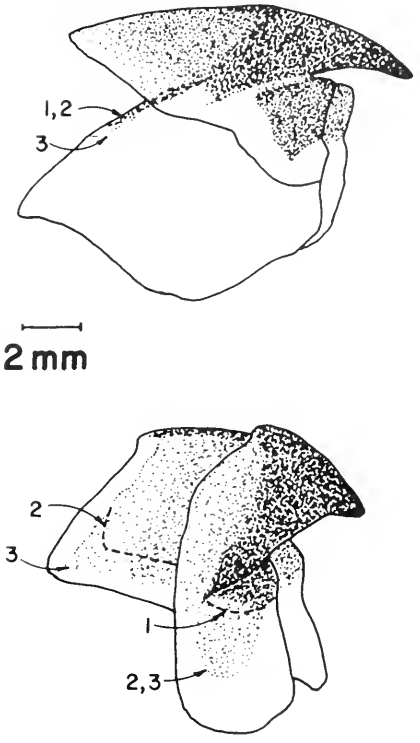


FIGURE 8.—The upper and lower beak of *Ommastrephes bartramii* (1 - ML = 85 mm, URL = 0.15 cm, LRL = 0.15 cm; 2 - ML = 140 mm, URL = 0.28 cm, LRL = 0.31 cm; 3 - ML = 165 mm, URL = 0.40 cm, LRL = 0.41 cm).

7a. HL/CL >0.825 (CI_{05} = 0.838±0.013); *RL/HL <0.344 (CI_{05} = 0.334±0.011); **RL/JW<1.188 (CI_{05} = 1.161±0.032) ..... *Dosidicus gigas*

Jaw angle deeply recessed; wing base inserted ½ way down anterior margin of lateral wall; two pigment stripes extend from the inner surface of the rostrum posteriorly onto the inner surface of the crest (Fig. 2)[3]; ridges and grooves more prominent than

[3]Rancurel, P. 1980. Note pour servir a la connaissance de *Symplectoteuthis oualaniensis* (Lesson 1830) (Cephalopoda, Oegopsida) : Variations ontogeniques du bec superieur. Cahiers de L'Indo-Pacifique 2(2):217-232.

pigment stripe in beaks with URL >0.60 cm; pigment changes with growth shown in Figure 9.

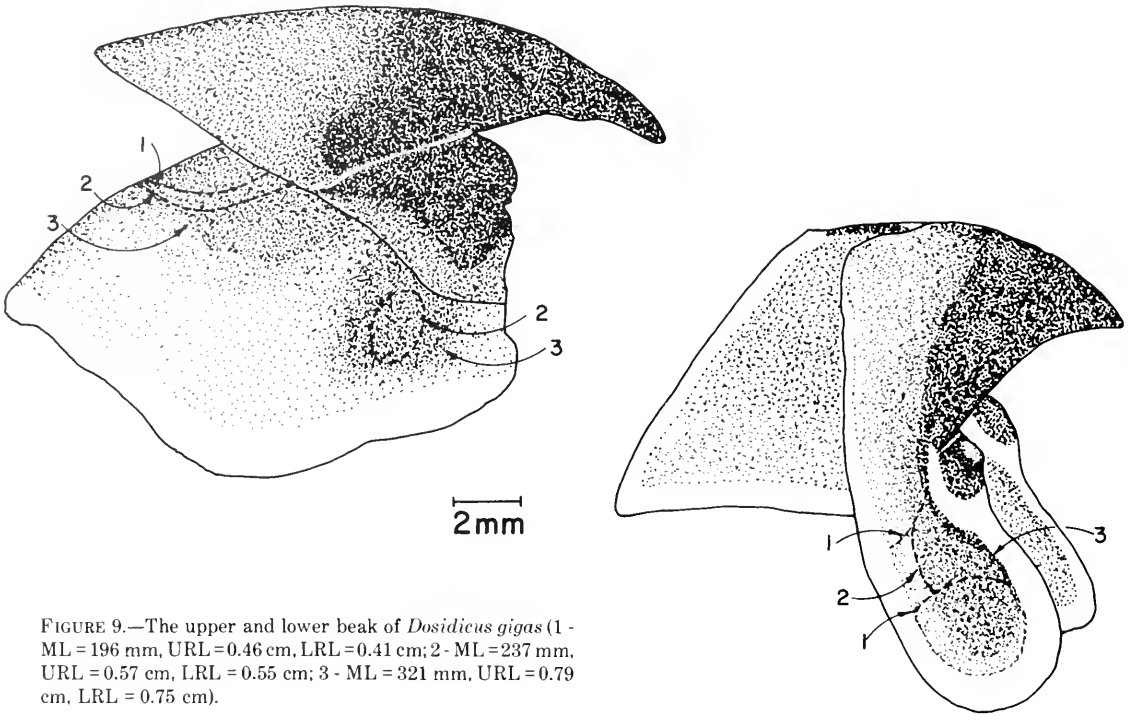
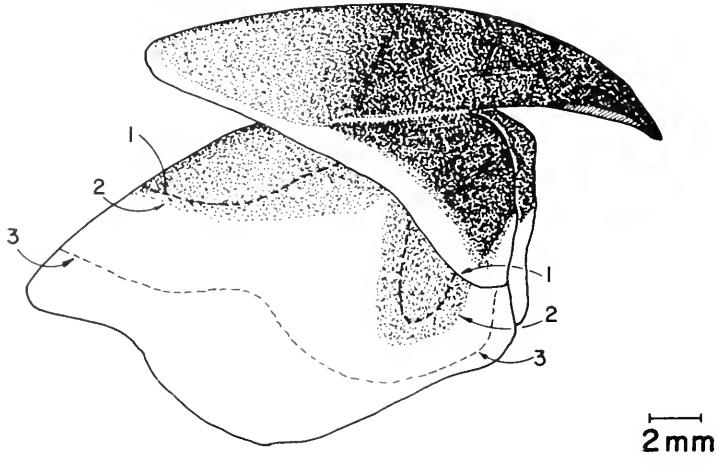


FIGURE 9.—The upper and lower beak of *Dosidicus gigas* (1 - ML = 196 mm, URL = 0.46 cm, LRL = 0.41 cm; 2 - ML = 237 mm, URL = 0.57 cm, LRL = 0.55 cm; 3 - ML = 321 mm, URL = 0.79 cm, LRL = 0.75 cm).

7b. HL/CL <0.825 (CI_{05} = 0.813±0.013); *RL/HL >0.344 (CI_{05} = 0.354±0.011); *RL/JW >1.188 (CI_{05} = 1.215±0.032) ..... *Symplectoteuthis oualaniensis*
Jaw angle deeply recessed; wing base inserted ½ down anterior margin of lateral wall; two pigment stripes present as in *D. gigas* (Fig. 2); ridges and grooves more prominent in beaks with URL >0.50 cm; pigment changes with growth shown in Figure 10.



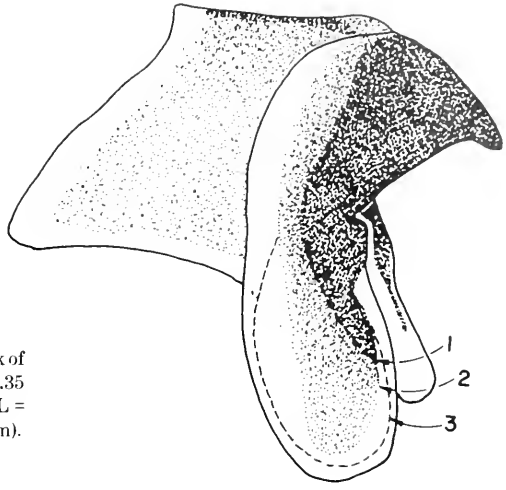


FIGURE 10.—The upper (see bottom of p. 366) and lower beak of *Sympleetoteuthis oualaniensis* (1 - ML = 130 mm, URL = 0.35 cm, LRL = 0.33 cm; 2 - ML = 188 mm, URL = 0.55 cm, LRL = 0.50 cm; 3 - ML = 290 mm, URL = 0.76 cm, LRL = 0.70 cm).

KEY TO THE LOWER BEAK

1a. Ridge or fold on lateral wall 2
1b. Ridge or fold absent on lateral wall 3

2a. RL/JW >1.173 (CI_{05} = 1.308±0.059); *RC/RL <3.091 (CI_{05} = 2.96±0.122) ..... *Abraliopsis affinis*
Jaw angle not recessed; no hood notch at crest; anterior-posterior ridge or fold on lateral wall[4] (Fig. 2); pigment changes with growth shown in Figure 4.
2b. RL/JW <1.173 (CI_{05} = 1.037±0.059); *RC/RL >3.091 (CI_{05} = 3.222±0.122) ..... *Onychoteuthis banksii*
Jaw angle not recessed; no hood notch at crest; prominent anterior-posterior ridge on lateral wall (Fig. 2); pigment changes with growth shown in Figure 3.

3a. Jaw angle strongly recessed 6
3b. Jaw angle slightly or not recessed 4

4a. RL/JW >1.134 (CI_{05} = 1.235±0.059); *RW/JW >3.565 (CI_{05} = 3.87±0.157) ..... *Liocranchia reinhardti*
Jaw angle slightly recessed; no hood notch at crest; pigment changes with growth shown in Figure 6.
4b. RL/JW <1.134 (CI_{05} = 1.032±0.059) 5

5a. RC/RL >3.741 (CI_{05} = 4.058±0.122); *RL/WL <0.418 (CI_{05} = 0.380±0.033) ..... *Loligo opalescens*
Jaw angle not recessed; no hood notch at crest; anterior margin of lower wing often produced; pigment changes with growth shown in Figure 7.
5b. RC/RL <3.741 (CI_{05} = 3.424±0.122); *RL/WL >0.418 (CI_{05} = 0.457±0.033) ..... *Pterygioteuthis giardi*
Jaw angle not recessed; no hood notch at crest; pigment changes with growth shown in Figure 5.

[4]A ridge or fold on the lateral wall of the lower beak is characteristic in many cephalopod species (e.g., *Histioteuthis* spp.).

6a. RL/WL >0.604 (CI_{05} = 0.632±0.033) 7

6b. RL/WL <0.604 (CI_{05} = 0.577±0.033); **RC/RL >2.890 (CI_{05} = 2.97±0.122) ..... *Ommastrephes bartramii*

Jaw angle recessed; no hood notch at crest (Fig. 2); pigment changes with growth shown in Figure 8.

7a. RL/JW >1.137 (CI_{05} = 1.197±0.059); **RC/JW >3.175 (CI_{05} = 3.360±0.189) ..... *Dosidicus gigas*

Jaw angle recessed; the hood is deeply notched at the crest (Fig. 2); pigment changes with growth shown in Figure 9.

7b. RL/JW <1.137 (CI_{05} = 1.077±0.059); **RC/JW <3.175 (CI_{05} = 2.990±0.189) ..... *Symplectoteuthis oualaniensis*

Jaw angle recessed; the hood is moderately notched at the crest (Fig. 2); pigment changes with growth shown in Figure 10.

The wet body weight and mantle length values for each species were used in linear regression equations to establish a relationship with a beak dimension. The regression equation has the form: $y = a + bx$, where y = weight or mantle length, $a = y$ intercept, b = slope of the regression line, and x = beak dimension. Initially a stepwise procedure, based on r^2 values, was used to determine if combinations of beak dimensions would improve the estimate. Adding more than one independent variable to the regression equations did not substantially increase the r^2 values of the body weight and mantle length equations.

The upper and lower beak of each species is represented by a pair of equations for mantle length and a pair of equations for body weight (Tables 4, 5). The first set of equations represents the best single independent variable equation derived from the stepwise regression procedure. The second set of equations retains the durable RL dimension of the upper and lower beak as the independent variable for all eight species. For the body weight equations all values were transformed to natural logarithms before regression.

DISCUSSION

The research on cephalopod beak ratios was initiated to determine whether species could be separated and identified by comparing different beak dimensions. Once this had been established, the primary use of such a technique was considered to be stomach content analysis. The condition of beaks removed from preserved, identified specimens is ordinarily much better than that of specimens removed from a predator's stomach. Therefore, other beak characteristics, in addition to maximum separation between species' means, were considered when the beak ratios for the key were selected. The selection was based on a dimension's durability under mechanical and chemical action, the effect such action would have on the accuracy of the beak dimension's measurement, and the ability to separate the ratio means at a given confidence level ($\alpha = 0.05$). Consequently, small dimensions with easily

TABLE 4.—Regression equations and r^2 values for mantle length and body weight, upper beak regression equations in centimeters, asterisk indicates best regression based on r^2.

Species	Mantle length (mm)	r^2	Body weight (g)	r^2
Symplectoteuthis	*ML = −2.17 + CL 105.2	0.95	*ln W = 3.7 + ln CL 3.1	0.98
oualaniensis	ML = −10.9 + RL 382.2	0.81	ln W = 7.6 + ln RL 3.2	0.95
Dosidicus	*ML = 65.8 + CL 86.2	0.95	*ln W = 4.3 + ln CL 2.23	0.97
gigas	ML = 41.1 + RL 346.8	0.87	ln W = 7.3 + ln RL 2.54	0.91
Liocranchia	*ML = −5.4 + JW 804.7	0.96	*ln W = 7.2 + ln JW 2.34	0.88
reinhardti	ML = −3.2 + RL 806.9	0.94	ln W = 7.0 + ln RL 2.22	0.87
Abraliopsis	*ML = 4.1 + CL 63.7	0.93	*ln W = 3.3 + ln CL 2.86	0.90
affinis	ML = 9.1 + RL 216.1	0.87	ln W = 6.0 + ln RL 2.2	0.85
Onychoteuthis	*ML = −22.1 + CL 127.6	0.92	*ln W = 9.4 + ln RL 3.8	0.93
banksii	ML = −31.0 + RL 641.0	0.87	ln W = 9.4 + ln RL 3.8	0.93
Pterygioteuthis	*ML = 2.1 + RW 230.9	0.76	*ln W = 3.8 + ln CL 2.75	0.87
giardi	ML = 7.3 + RL 289.8	0.62	ln W = 5.8 + ln RL 2.04	0.83
Ommastrephes	*ML = 42.4 + HL 95.8	0.99	*ln W = 3.7 + ln CL 2.4	0.98
bartramii	ML = 51.4 + RL 282.4	0.94	ln W = 6.7 + ln RL 2.15	0.96
Loligo	*ML = −5.7 + CL 153.5	0.94	*ln W = 6.0 + ln RW 2.25	0.80
opalescens	ML = 42.2 + RL 542.7	0.79	ln W = 5.7 + ln RL 1.21	0.65

TABLE 5.—Regression equations and r^2 values for mantle length and body weight, lower beak regression equations in centimeters, asterisk indicates best regression based on r^2.

Species	Mantle length (mm)	r^2	Body weight (g)	r^2
Symplectoteuthis	*$ML = -11.93 + RC$ 115 4	0.96	*ln $W = 4.7 +$ ln RC 3.2	0.98
oualaniensis	$ML = 6.98 + RL$ 392.5	0.93	ln $W = 7.8 +$ ln RL 3.0	0.96
Dosidicus	*$ML = 68.0 + WL$ 207.7	0.95	*ln $W = 4.97 +$ ln RC 2.3	0.95
gigas	$ML = 44.2 + RL$ 357.9	0.84	ln $W = 7.4 +$ ln RL 2.48	0.91
Liocranchia	*$ML = 0.85 + JW$ 956.8	0.94	*ln $W = 7.76 +$ ln JW 2.3	0.88
reinhardti	$ML = -1.09 + RL$ 802.2	0.89	ln $W = 6.7 +$ ln RL 2.1	0.80
Abraliopsis	*$ML = 6.3 + RC$ 77.7	0.95	*ln $W = 3.8 +$ ln RC 2.5	0.91
affinis	$ML = 9.8 + RL$ 192.8	0.88	ln $W = 5.5 +$ ln RL 2.1	0.81
Onychoteuthis	*$ML = -22.5 + RC$ 177.7	0.93	*ln $W = 4.7 +$ ln RC 3.5	0.94
banksii	$ML = -28.9 + RL$ 610.0	0.95	ln $W = 9.1 +$ ln RL 3.7	0.89
Pterygioteuthis	*$ML = 2.3 + RC$ 121.9	0.76	*ln $W = 4.5 +$ ln RC 2.7	0.92
giardi	$ML = 6.2 + RL$ 331.6	0.41	ln $W = 7.6 +$ ln RL 2.6	0.70
Ommastrephes	*$ML = 44.6 + RC$ 103.5	0.99	*ln $W = 4.4 +$ ln RC 2.3	0.99
bartramii	$ML = 52.7 + RL$ 276.1	0.96	ln $W = 6.6 +$ ln RL 2.07	0.98
Loligo	*$ML = 6.0 + RW$ 240.9	0.87	*ln $W = 4.4 +$ ln RC 1.95	0.76
opalescens	$ML = 32.4 + RL$ 607.8	0.74	ln $W = 6.0 +$ ln RL 1.4	0.58

damaged margins (e.g., RW, WW upper beak) were excluded from consideration when constructing the key, even though they might show very good separation between species' means when used in a ratio (e.g., RL/RW upper beak). Larger dimensions which have easily damaged margins (e.g., CL/HL) can still provide a reliable dimension within the variability of the sample simply because the eroded margin represents less of the overall dimension compared with the smaller dimension with similar properties.

Accurately determining which cephalopods are abundant in an area and which of these might be important in a predator's diet are difficult problems to solve. The abundance of a species in a trawl sample is not necessarily an accurate reflection of its relative abundance in the field (Wormuth 1976) or in a predator's stomach (Clarke 1977). In an attempt to reduce this sampling bias the cephalopods in this study were chosen on the basis of their abundance in trawl samples (Young 1972; Okutani 1974), in collections using alternate sampling devices (e.g., dip nets and jigs (Wormuth 1976)), and in stomach content studies of cephalopod predators in the same area (Pinkas et al. 1971; Perrin et al. 1973).

The eastern tropical Pacific is the area for which these beak characterizations were constructed. In many cases, large, pelagic cephalopod predators in this area will contain a large percentage of the species described in this study. As one moves away from this area, however, less can be said about the potential usefulness of this key, since the species composition and morphological characteristics, including beak dimensions, can change. As an example, 28 specimens of *O. bartramii* from the Gulf of Mexico and northwestern Atlantic have an upper rostral length to jaw width ratio mean (RL/JW) of 1.22 ($CI_{05} = \pm 0.02$); considerably greater than the eastern tropical Pacific mean of *O. bartramii* ($\bar{x} = 1.06$, $CI_{05} = \pm 0.03$). This higher ratio value also holds for three specimens from southeastern Australia.

Such geographical variation in species with disjunct distributions is not uncommon and has been noted in other body measurements for *O. bartramii* by Young (1972). Additional measurements must be made on remaining cephalopod species in this key, particularly those with disjunct distributions, before this key can be reliably used outside the eastern tropical Pacific area.

There will be cephalopods in the stomachs of predators which are not included in this work. In order to reduce misidentifications, therefore, full use should be made of the alternate ratio means, the beak figures, and the descriptive characteristics.

In most beaks, the dimensions which resulted in the best regression equations for mantle length and body weight were those that were close to the overall length of the beak (CL, HL, RC). In badly damaged beaks, however, these dimensions are often in poor conditon. The pairs of regression equations for each of the eight species represent an effort to increase the flexibility of estimating the size of a cephalopod. The regression equations which use the RL dimension variable will give less accurate estimates, but can be used in all but the most severely damaged beaks, as the RL is a very durable dimension.

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MOVEMENT AND SPEED OF DOLPHIN SCHOOLS RESPONDING TO AN APPROACHING SHIP

D. Au and W. Perryman[1]

ABSTRACT

Eight dolphin schools of the species *Stenella attenuata*, *S. longirostris*, and *S. coeruleoalba* were approached by ship and observed from a helicopter in the eastern Pacific to study their response to the vessel. All schools swam away from the projected track of the aproaching ship. Their movement, relative to the ship, followed paths that curved around the ship. Average swimming speeds while avoiding the ship varied from 5.1 to 8.8 knots. In some cases avoidance apparently began at 6 or more miles away from the ship. The effect of this behavior on shipboard censusing of dolphins is discussed.

In the eastern tropical Pacific, tuna fishermen encircle with purse seine nets schools of certain small cetaceans, mainly spotted and spinner dolphins, *Stenella attenuata* and *S. longirostris*, to capture the yellowfin tuna, *Thunnus albacares*, with which they are associated (Perrin 1969, 1970). The resulting incidental kill of dolphins has led the National Marine Fisheries Service to study the status of these cetacean populations, as required by the Marine Mammal Protection Act of 1972. Data collected from commercial fishing boats and research vessels are important in determining the distribution and abundance of the dolphins.

In the areas of intensive "porpoise fishing," dolphins are apparently learning from their experience with nets and fishing vessels. The animals are recaptured with purse seines frequently enough to have possibly learned to position themselves within the net to better facilitate their own release (Pryor and Kang[2]). More importantly, they may also have developed various behaviors to avoid detection by a fishing vessel and to reduce their chances of capture (Pryor and Kang footnote 2; Stuntz and Perrin[3]). Dolphin schools, especially of the spotted and spinner dolphin species, commonly swim rapidly away from approaching ships. This behavior is our usual observation when studying dolphins from research ships.

In November 1976 we conducted a study to describe ship-avoidance behavior of dolphins. The purpose was to quantitatively describe school trajectories around an approaching ship and to evaluate the effect on shipboard censusing of dolphins. This study also allowed us to measure the swimming speeds of the schools and to make observations on school structure and behavior.

METHODS AND MATERIALS

We conducted this study from the NOAA Ship *Surveyor*, a 300-ft (91.4 m) steam-powered research vessel, and its Bell[4] 204 helicopter. We worked in the study area, the vicinity of Clipperton Island (lat. 10°15'N, long. 109°10'W) in the eastern Pacific, for 9 d (26 November to 4 December 1976). During six of these days, we made observations from the helicopter, flying twice daily in a crossing pattern ahead of the ship's track (Fig. 1). This enabled us to detect dolphin schools ahead of the ship and to follow the sequence of events leading to avoidance or the detection of the school by the shipboard observers. The 2.5-h flights began in mid-morning (ca. 0900 h) and early afternoon (ca. 1330 h) to take advantage of the best lighting conditions for aerial observations and photography. Air speed was about 80 kn (1 kn = 1.85 km/h) at altitudes between 1200 and 1800 ft (366-

[1]Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

[2]Pryor, K., and I. Kang. 1980. Social behavior and school structure in pelagic porpoises (*Stenella attenuata* and *S. longirostris*) during purse seining for tuna. Southwest Fish. Cent. Admin. Rep. LJ-80-11C.

[3]Stuntz, W. E., and W. F. Perrin. Learned evasive behavior by dolphins involved in the eastern tropical Pacific purse seine fishery. (Abstr.) Third Conference on the Biology of Marine Mammals, Seattle, Wash., October 7-11, 1979.

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

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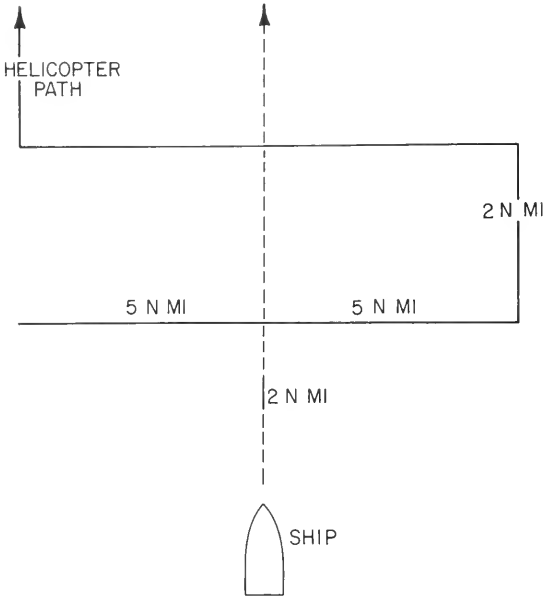

FIGURE 1.—Path of helicopter in front of ship during search phase of study.

549 m). Maximum altitude was determined by the cloud ceiling. During each flight, two scientific observers aboard the ship searched independently with 20 × 120 mm binoculars for dolphins. The observers were not in communication with the helicopter and were generally unaware of its position because of its range and because of their visual concentration on the sea surface. The ship's speed was between 11 and 13 kn.

Once a school was located, the helicopter remained near the school to serve as a radar target to fix the position of the dolphins relative to the vessel. Each time the helicopter passed over the school, we signaled the deck officer aboard ship via radio to record our radar range and bearing. These measurements from the ship were taken at successive time intervals to enable tracking the movement of the school. There was no indication to us that the helicopter affected school behavior. Indeed, the schools usually appeared to be swimming calmly throughout the tracking, until the ship approached to within a mile of the dolphins. During this tracking phase, ship course changes were minimized in order to determine how closely the school would pass the approaching vessel if not pursued. In some cases the ship was turned so its projected track would pass near the school, but course changes were minimal thereafter.

The shipboard radar used was a Decca-RM 1630. Its rated accuracy is to within 300 yd (274 m) of range at a distance of 10 nmi (18.5 km) and to within 1° of angular bearing. The radar measurements were made by a trained deck officer.

At the end of the tracking phase the ship approached closely or followed each school until the observers aboard had completed their estimates of school size and species composition. Meanwhile, we continued to take aerial photographs (35 and 70 mm still and 16 mm movie) and notes on school size and behavior that had begun when the school was first sighted. The movements and speeds of the schools as described below do not refer to this last phase of the operation.

School movement and speed were calculated whenever possible from relative motion plots since such plots portray the situation as seen from a ship. Required information for each plot includes the time interval between radar fixes, the course and speed vector of the ship, and the relative motion vector of the school, as determined by the radar ranges and bearings (the method is described by Bowditch 1966). These data were then used to construct vector triangles which were solved to get school speed vectors. Distance (range) was measured in nautical miles (nmi) and speed in knots (kn). The results were checked by plotting the sequential, absolute positions of the vessel and school from the data on vessel speed and data on range and bearing of ship to helicopter (school). School movement was measured from this absolute plot, and speed determined from the time interval between fixes to give results that should be the same as those obtained from the relative motion plots. When the ship made a course change, disrupting the relative position analysis for that time interval, the absolute position plot was the only solution.

A hypothetical example of a relative motion plot is presented in Figure 2. The ship is at the center (0) of the polar plot, proceeding straight ahead (000° or top of plot). Sequential radar ranges and bearings, from the moving ship to a dolphin school, are obtained at 0800, 0815, ..., and 0900 h. These fixes are plotted, and the line connecting them shows the relative motion of the school that is passing around to the right of the ship. The actual swimming vectors of the school, which produce this relative motion, can be obtained by solving vector triangles such as that shown at the center of the plot. For example, the

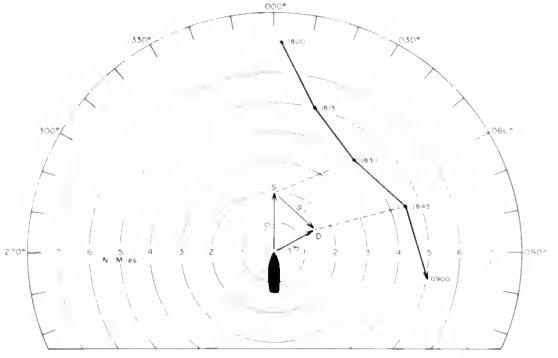

FIGURE 2.—Example of relative motion plot and calculation of school swimming vector.

relative motion between 0830 and 0845 h is equivalent to a relative velocity vector of 9.1 kn heading 134°. Projecting this vector (SD) onto the ship's vector (OS), which is 10 kn heading 000°, the school's swimming vector (OD) is obtained by vector subtraction as shown. In this case the swimming vector is 7.5 kn, heading 060°, and is the average swimming velocity between 0830 and 0845 h. Notice that the relative motion line is defined by ranges and bearings while the triangle at the center is composed of speed vectors, where, for convenience, 10 kn is defined as having magnitude 0 to 2 on the mile scale.

RESULTS

Vessel Avoidance

We were able to follow eight dolphin schools with the ship and helicopter (Table 1). The species were the spotted dolphin, the spinner dolphin, and the striped dolphin, *S. coeruleoalba*. All eight schools continuously adjusted their

TABLE 1.—Summary of dolphin schools observed from helicopter.

School	Species	Date and position	Local time (h)	Initial Range (nmi)	Initial Speed (kn)	School[1] size	Behavior relative to distance from ship[2]
1	*Stenella attenuata* + *Stenella longirostris*	11-26-76 (11°54'N 107°13'W)	0950	5.6	5.8	100	At 3.5 mi ship changes course and school increases speed to 8.3 kn. Between 1.9 and 2.6 mi school veers 40° to right across ship's path; as ship's path is crossed, school alters course again to head directly ahead of ship. At 2 mi school is in 2 groups running very purposefully with little intraschool deviations. Cruising smoothly at 5-6 kn with little splashing during most of vessel approach; strong evasive maneuvers at 100 m by group closest to ship. Two species incompletely mixed, many adults and juveniles in school.
2	*Stenella coeruleoalba*	11-27-76 (8°27'N 107°07'W)	0938	6.2	4.3	50	School initially "porpoising" gently as a loose aggregation, moving away to ship's right. At ca. 6.0 mi ship changes course; school veers 108° to left, accelerating to 5.8 kn. At ca. 5.0 mi school turns left again, still moving away at ca 5.5 kn. At ca. 3.3 mi ship changes course and school accelerates to 6.3 kn temporarily. Between 2.0 and 3.0 mi school turns more to left; still running smoothly at 5.5 kn with little splashing. As ship passes 2.0 mi to right of school, it veers sharply left, continuing on almost opposite course as ship. Individuals bunching up at 1.8 mi. At times school composed of 4 groups. At 1.5 mi school speed is 8.3 kn. At 0.9 mi school running smoothly ahead of ship; a portion breaks off to right at ca. 100 m distance.
3	*Stenella attenuata*	12-1-76 (10°00'N 108°01'W)	0935	5.2	6.4	15	School initially seen under ca. 100 feeding boobies (*Sula* sp.), moving away from ship. At ca. 4.3 mi school accelerates to 7.8 kn then slows to 6.2 kn. At 3.5 mi school turning to right. Between 2.0 and 3.0 mi school swimming smoothly at ca 5.0 kn; birds flying, rafting, or diving; most working ahead of school; later they form 2 large rafts behind school. By 1.5 mi school speed has increased to 7.2 kn. As school passes to left of ship at ca 1.5 mi, it accelerates to 13 kn and veers to left. Birds have ceased feeding inside of 2 mi distance. School begins strong evasive maneuver at ca. 1/4 mi distance.
4	*Stenella attenuata*	12-2-76 (9°30'N 109°39'W)	0823	6.2	3.8	350	Initially detected as bird target by radar. Between 4.2 and 4.9 mi school changes course sharply away from ship, increasing speed to 4.6 kn, then slowing to 2.9 kn. At 3.0 mi much splashing in running school; some long, flat leaps seen. School becoming more scattered. Birds toward rear of school, later are scattered over school. At ca. 3.2 mi ship makes 90° turn to left; school veers 94° to left and increases speed; much running leaps seen; by 3.0 mi school speed is 6.5 kn. Between 2.5 and 3.0 mi main group in school turns toward ship; moments later they reverse their course again.

directions of swimming, by small increments, so that the distance between the school and the ship's projected track tended to increase continuously with time. The schools were either already proceeding on courses directed away from the ship when first sighted or made sharp course changes away from the vessel soon after. Several schools were moving off at relatively high speed when first seen. All the schools were evidently avoiding the ship. The behavior that indicated avoidance is summarized in Table 2 for each school. It appeared that avoidance behavior sometimes had begun when the school was still 6 or more nautical miles away from the ship.

Sufficient positioning data were collected from six of these schools to prepare diagrams of their movement relative to the approaching ship (Figs. 3, 4). The first school, school 1, is not plotted because frequent course changes by the ship during its tracking made relative movement difficult to portray. The path of relative movement of any of these schools, drawn by connecting the sequential series of radar fixes of the school as the ship moved forward, does not

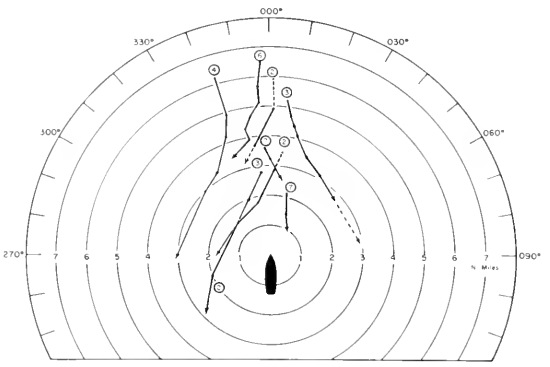

FIGURE 3.—Relative movement plots of five schools (nos. 2, 3, 4, 6, 7), showing the apparent motion as seen by a shipboard observer. Dotted lines are by dead reckoning.

TABLE 1.—*continued.*

School	Species	Date and position	Local time (h)	Initial Range (nmi)	Initial Speed (kn)	School[1] size	Behavior relative to distance from ship[2]
							At 2.5 mi individuals begin to bunch up; school in form of large arc with some scattered animals on the sides; birds no longer feeding.
							At 1.6 mi school is again scattered. Within 0.5 mi parts of school breaking away from ship's path; birds rafting nearby.
5	*Stenella attenuata* + *Stenella longirostris*	12-2-76 (9°39'N, 109°48'W)	0953	5.8	ca. 2.6	300	Initially seen with many birds ahead and to right of school. School speed is ca. 2.6 kn.
							At 3.3 mi school changes course sharply away from ship and speed accelerates. Animals running with compact ranks at rear of school; few birds over school now.
							At 3.0 mi school running smoothly at ca. 8.4 kn.
							At 2.2 mi individuals appear confused, going in various directions within oval shaped school.
							At 2.0 mi a group temporarily heads toward ship before reversing course; school speed is 9.3 kn.
							At 0.6 mi many circuitous movements seen among small subgroups. School passes to ship's left; all individuals uniformly running from ship at 8-9 kn; birds rafting ahead.
							Ship turns toward school at ca. 0.5 mi; school splits ahead of ship at ca. 200 m; each dolphin species goes to different side of ship.
6	*Stenella attenuata*	12-3-76 ca. (9°31'N, 110°30'W)	1032	6.9	ca. 10.0	40	School initially seen as running, oval mass moving off at ca. 10.0 kn with much splashing.
							At 6.5 mi school is in 2 groups moving smoothly in arc with little splashing.
							At 5.7 mi school is in 2 groups moving smoothly at 8.5 kn.
							At 5.1 mi school is composed of a dense and a scattered section; many direction changes among subgroups. School speed is down to 7.0 kn.
							At 4.5 mi school is scattered; composed of 3 large groups; many direction changes seen; speed is ca. 9.0 kn again.
							Between 3.5 and 4.0 mi school speed decreases to 7.6 kn then increases to 9.3 kn as school begins passing to ship's left.
7	*Stenella attenuata* + *Stenella longirostris*	12-3-76 (10°00'N, 110°30'W)	1440	3.6	8.8	150	Initially swimming smoothly at ca. 8.8 kn with little splashing; scattered individuals at rear of school.
							At ca. 3.0 mi school still holding similar course with speed of ca. 7.0 kn; 50-70 birds over school.
							At 2.4 mi ship changes course and school also changes course and increases speed; birds scattered over the scattered school.
							At 1.4 mi school running smoothly in loose groups, going ca. 6.0 kn.
							At <1.0 mi smoothly running school is scattered by ship.
8	*Stenella coeruleoalba*	12-2-76 (10°27'N, 110°01'W)	1420	0.9	—	65	A leaping, loosely aggregated school at 0.9 mi.
							At 0.7 mi school running with increasing speed as ship turns toward school.
							At 1/4 mi school forming an arc ahead of ship.

[1]Estimated from aircraft.
[2]Distances and behavior from radar ranging and bearing, interpolation of movement trajectories, and field notes. Distances in nautical miles.

TABLE 2.—Range and behavior when vessel avoidance was first seen.

School number	Species	Range (nmi)	Behavioral indication of vessel avoidance
1	*S. attenuata* *S. longirostris*	5 6	School rapidly swimming away from ship at 5 8 kn when first sighted from helicopter
2	*S. coeruleoalba*	ca 6 0	As ship turned toward this school, the animals accelerated from 4.3 to 5 8 kn and turned away from the ship.
3	*S. attenuata*	5 2	School rapidly swimming away from ship at 6.4 kn when first sighted from helicopter
4	*S. attenuata*	ca 4 6	School made sharp course change away from ship and accelerated to 4 6 kn.
5	*S. attenuata* *S. longirostris*	3.3	School turned away from ship and accelerated from 2 6 to 8 4 kn.
6	*S. attenuata*	6.9	School moving away from ship at high speed (ca 10 kn) when first sighted from helicopter
7	*S. attenuata* *S. longirostris*	3.6	School moving away from ship at high speed (8.8 kn) when first sighted from helicopter
8	*S. coeruleoalba*	0.9	School leaping away from ship when first sighted from helicopter.

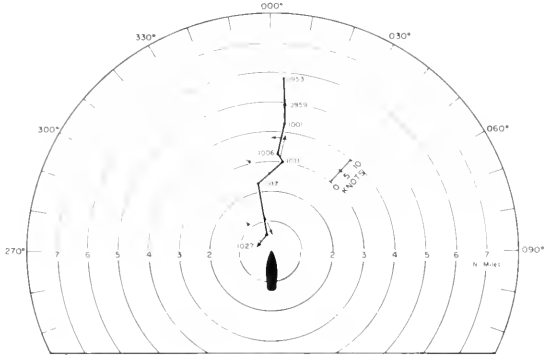

FIGURE 4.—Relative motion plot of school 5, showing its apparent motion as seen by a shipboard observer. Small arrows show actual school velocities at various distances. Note heading reversal shown at 1.5 mi.

represent the actual swimming directions of the school, but rather the resultant of the swimming velocity of the school and the movement of the vessel. The ship's position remains at the center of each diagram, and swimming direction is depicted relative to the ship's heading, which is toward the top of the page. The plots therefore show the apparent motion of the schools as seen by an observer aboard the ship. A break in the relative motion line for a school represents a course change by the ship.

The relative movement of five schools (schools 2, 3, 4, 6, and 7) are depicted in Figure 3 where, for clarity, swimming speed vectors and the times of radar fixes are not included. It is important to realize however, that along each relative motion line the school is generally swimming away from the oncoming ship. We have extrapolated parts of the movements of schools 2 and 3, based upon our observations of their activity. The movement of each of the five schools is depicted as though moving relative to the same ship heading (000°). These schools are described in two groups.

The first group (schools 2, 3, 4, and 6 in Figure 3) was initially located between 5 and 7 nmi from the ship. After some initial adjustments in heading, the schools' swimming directions remained relatively constant. The resultant paths of the dolphin schools thus veered from the track line at a nearly constant angle after this initial period. Assuming that the schools would remain approximately on the same course and extending their lines of relative movement, it appeared that these schools would have passed no closer than 2.4 nmi from the ship, had it remained on the same course. School 4 exhibited additional notable behavior that is not shown in Figure 3. When the school had passed abeam, the ship was turned towards the school. Five minutes later, at a range of about 2.5 nmi, a large section of the school turned and headed toward the ship in a tightly aggregated group. Within a minute this section reversed course again and rejoined the original school.

The second group (schools 2, 3, and 7 in Figure 3) consists of schools that were between 2.6 and 3.7 nmi away, either when first sighted (school 7) or after the ship had turned toward the school at the end of an initial tracking period (schools 2 and 3). The lower and separated segments of the latter schools' tracks represent the relative movements after the ship had turned. These schools were then within 0.4 nmi of the ship's projected track. Even so schools 2 and 3 subsequently came no closer than 1.4 nmi to the ship. School 7, by its initial projected trajectory, would have come no closer than 1.5 nmi, but after the ship turned toward it, its new resultant path would have taken it about 0.7 nmi from the ship.

School 5 behaved quite differently from the others. Both relative movement, time of radar fixes, and swimming speed vectors are shown for this school (Fig. 4). The swimming speed vectors, shown as arrows attached to the relative motion line between various time and distance intervals, are drawn proportional to the calculated swimming speeds (Table 3).

School 5 was probably feeding when the bird flock associated with it was first detected on the ship's radar at a distance of 5.8 nmi. The distance and bearing plots of the birds indicated erratic movement. Later, in the tracking-by-helicopter phase, the first two ranges and bearings showed the school moving at only 2.6 kn. The inferred feeding behavior from this is consistent with the feeding behavior described by Norris et al. (1978), as well as other observations by us in the eastern Pacific. At a closer range of about 3.3 nmi from the ship, the school's behavior changed radically as it altered course by 97° to the right and increased its speed to 8.4 kn, turning on a course that would have taken it 2.0-2.5 nmi abeam of the passing ship. Between 2.3 and 3.0 nmi the school again shifted course, this time by 70° to the left, and increased its speed to 9.4 kn. When this school reached a point about 0.5 nmi from the track line and 2.3 nmi from the ship, its behavior changed again. Individuals and subgroups within the school began swimming in many different directions, making large changes in course heading. Suddenly the main body of the school turned nearly 180° and swam toward the ship at high speed (~9 kn). After closing to within 1 nmi of the ship, the school reversed itself again, and thereafter swam rapidly away from the vessel. This type of "error" in choice of avoidance heading was only seen in schools 4 and 5, which were both relatively large schools (300-350 individuals estimated).

School Speed

While avoiding the ship, the speeds of the first seven schools varied between 2.5 and 13.1 kn, with average speeds between 5.1 and 8.8 kn (Table 3). The eighth school was too close to the ship for ranging measurements by radar. There was no apparent difference in swimming speeds among the three species observed. Substantial variation in speed occurred in all seven schools. Schools 1, 2, 3, and 4 swam at speeds that averaged between 5 and 7 kn. Schools 6 and 7 had the

TABLE 3.—School swimming speed vectors.

School	Time (h)	Range[1] (nmi)	Bearing[1]	Course[2]	Speed[2] (kn)
1	0950	5.6	088°		
	1015	3.6	105	128.2°	5.8
	1022	3.3	107	128.6	8.3
	1030	2.6	104	126.3	5.7
	1035	1.9	112	166.7	5.3
	1042	1.4	115	114.5	6.2
	1049	0.8	110	100.0	6.8
	1101	0.7	310	092.0	4.0
					[3]$\bar{x}$=6.0
2	0938	6.2	016		
	0942	5.9	026	118.3	4.3
	0952	4.9	026	010.6	5.8
	1000	3.7	017	330.7	5.5
	1006	2.9	008	324.6	6.3
	1013	1.8	352	304.6	5.5
	1019	1.5	320	315.2	8.3
	1028	2.0	255	285.2	5.7
	1033	3.0	230	216.5	5.6
	1045	2.5	212	223.6	6.0
	1051	2.0	200	229.0	5.9
	1104	0.9	179	182.8	6.3
					$\bar{x}$=5.9
3	0935	5.2	295		
	0940	4.7	297	300.9	6.4
	0943	4.4	299	308.9	6.5
	0947	4.1	301	298.8	7.8
	0953	3.5	308	316.6	6.2
	0959	3.1	320	326.2	7.8
	1006	2.8	340	335.1	6.2
	1016	2.9	019	354.2	5.0
	1023	2.0	010	337.0	[4]4.9 (1017-1023)
	1029	1.6	353	005.0	6.6
	1032	1.5	335	334.5	7.2
	1035	1.8	296	264.0	13.1
					$\bar{x}$=7.1
4	0823	6.2	333		
	0829	4.9	333	086.5	3.8
	0835	4.2	330	349.5	4.6
	0841	3.2	318	261.9	2.9
	0845	3.0	305	282.5	6.5
	0857	3.2	256	263.2	5.2
	0915	1.6	255	265.8	6.2
					[4]$\bar{x}$=5.1 (0835-0915)
5	[5]1001	4.3	356		
	1006	3.3	354	264.2	2.6
	1011	3.0	357	001.2	8.4
	1017	2.3	339	290.8	9.4
	1022	0.6	334	148.4	9.3
	1027	0.5	268	314.7	7.9
					[4]$\bar{x}$=8.8 (1011-1027)
6	1032	6.9	281		
	1038	6.5	278	273.6	10.0
	1050	5.7	277	279.2	8.5
	1056	5.1	277	284.4	7.0
	1102	4.7	273	262.0	9.2
	1108	4.3	270	270.1	8.8
	1112	3.9	271	297.4	7.6
	1121	3.4	258	253.3	9.3
					$\bar{x}$=8.6
7	1440	3.6	167		
	1446	3.2	170	182.4	8.8
	1452	2.6	177	199.1	6.6
	1458	2.1	191	215.3	7.5
	1505	1.4	197	175.6	6.0
	1508	1.0	205	164.6	2.5
	1519	1.1	240	242.0	11.5
					$\bar{x}$=7.2

[1]Range and bearing of school from ship at times appropriate to the speed calculation. If notable, behavior at these and other times are reported in Table 1.
[2]Speed vectors pertain to time intervals ending at times listed unless otherwise indicated. Calculations are from relative or absolute plots involving ship motion.
[3]Mean school speed refers to times when school is responding to ship.
[4]Time interval for this calculation.
[5]This school was actually sighted at 0953, but measurements did not begin until 1001

highest initial speeds, 10.0 and 8.8 kn, respectively, and had average speeds of 8.6 and 7.2 kn, respectively. Both were moving with the waves in a Beaufort 4 sea state (11-16 kn wind) and were probably utilizing the forward momentum of the swell as described by Lang (1975). The speed of school 5 was also high (>8 kn) after the first 5 min that it was observed. Its average speed while actively avoiding the ship was 8.8 kn. This higher sustained speed may have been related to its level of excitement that was evident in its apparently confused state, when it turned toward and then away from the ship (Table 1, Fig. 4). Schools 3 through 7 showed some tendency for increased speeds as the ship drew nearer.

Swimming Behavior and School Structure

Field descriptions of each school, and later study of the aerial movie and still photographs, revealed no obvious indication of dominant, or leading, individuals or subgroups. The schools were seen to progress in an almost amoeboid fashion with subgroups of two to five individuals striking off in different directions or accelerating to higher speeds, then drifting back to the main body of the school if not followed by others in the school. Although individuals and subgroups within a school were constantly changing course, sometimes abruptly, the heading of the main body of the school remained nearly constant or changed slowly. The schools appeared as loose aggregations of individuals and small subgroups, most proceeding along similar headings. Individualistic rather than coordinated movements were the general feature of these schools. The schools appeared to be one-layered, i.e., groups of animals were not swimming beneath others.

As the vessel closed to within 2 nmi of the schools, the subgroups within the schools were seen to be increasingly oriented in lines abreast. Animals in the rear third of a school could be seen swimming faster than those ahead. The result was that the width of a school in the direction of its swimming axis narrowed as the distance between ship and school decreased.

DISCUSSION

Our first impression from the observed school behavior and structure was that the dolphins were not noticeably disturbed by the vessel's presence. Only at a distance of less than a mile did bunching or compaction of the relatively dispersed individuals and small subgroups become common and did the schools obviously appear to be running, i.e., in flight (Table 1). Radical, evasive maneuvers were not regularly seen until the last 200 m of distance between ship and school. Examination of the relative motion plots and the consecutive vectors of swimming speed and course made it clear, however, that the dolphins were actually avoiding the ship much earlier, sometimes beginning at distances approaching the horizon for a shipboard observer. Though ship-avoidance behavior should not be surprising, considering the extent of "porpoise fishing," in the study area, it is a behavior not easily studied from a surface platform. These observations have important implications relative to population studies of dolphins, especially those conducted from ships.

Because a shipboard observer sees a dolphin school increasingly in profile view as distance increases, an understanding of its structure and behavior is helpful for proper interpretation of its characteristics. A travelling school appears to be a loose aggregation of relatively widely separated individuals or subgroups of 2-5 animals. Rather than being made up of relatively few, tight subgroups of various sizes, as observed for spotted dolphins in a purse seine (Norris et al. 1978), most of the animals in these schools appeared to be swimming independently, as individuals or in pairs. This school configuration appeared typical all during vessel avoidance, except at radial distances of less than a mile from the ship.

The schools we observed remained inconspicuous to the shipboard observers because they swam smoothly, without much splashing, at speeds that averaged 6.8 kn. Even at swimming speeds of 7-9 kn, the animals often broke the water surface with little commotion and swam most of the distance between breaths just under the surface. Bursts of higher speed, with attendant long leaps (2-3 body lengths) and large splashes, occurred only temporarily.

The swimming speeds presented in Table 3 pertain to these pelagic dolphins when swimming in the cruising mode, i.e., moving smoothly with little splashing for sustained periods. The higher observed speeds of 7-9 kn are still in the upper range for prolonged cruising speeds of smaller dolphins (Webb 1975). That this must be so is indicated by the fact that research ships

moving at 10 kn can always closely approach these dolphins, provided that the schools can be followed. Evidently school speeds greater than that of the ship can be maintained only temporarily. Dolphins that do break into the "running," or leaping swimming mode, must be exceeding a certain "crossover speed." This is the swimming speed above which a leaping locomotion becomes more efficient. It is calculated to be somewhat in excess of 10 kn (Au and Weihs 1980). Thus several lines of evidence indicate that cruising speeds are <10 kn, as we in fact measured. Dolphins of course are capable of temporary higher speeds than reported here. Top burst speeds as high as 14.5 kn have been measured for *Tursiops truncatus* (Lang and Norris 1966) and 21.4 kn for *S. attenuata* (Lang and Pryor 1966).

Because the faster, leaping locomotion produces much splashing, dolphins that avoid ships by moving away more slowly at cruising speed obviously are more difficult to detect from the ships. The initial avoidance probably proceeds at cruising speed because the dolphins are not yet highly alarmed at the distances at which detection of the ship and evasion begins.

The evasive behavior of dolphins perhaps has its most important implication relative to school density studies conducted from ships. In particular the line-transect method (Seber 1973; Burnham and Anderson 1976), which can be employed for absolute density estimation of schools, may be affected. An important requirement of the method is that the schools do not move, or move randomly or little, relative to the speed of the observer. However, schools are evidently capable of avoidance movements at speeds approaching that of the ship. Therefore positions of schools relative to the ship and prior to movement that are required to describe the probability of sighting a school cannot be obtained if there is movement. Only if the school trajectories were known could the observed positions be corrected. The probability of sighting is usually obtained from the distribution of perpendicular distances that are a transformation of the relative positions of sighted schools. Laake (1978) and Burnham et al. (1980) emphasized that when school movement occurs, both the probability functions describing detectability and the altered animal distribution are completely confounded in the distribution of observed perpendicular distances. School movement also violates the critical assumption that all schools initially on the track line will be seen. Therefore, line transect methods for absolute density estimation usually cannot be used when avoidance movements occur.

It is easy, however, to understand how avoidance behavior reduces the probability of sighting a school from a ship. Without movement this probability would be (Burnham and Anderson 1976)

$$\frac{1}{w}\int_0^w g(x)dx$$

where w is the half width of the swath being searched, which could be the horizon distance, and $g(x)$, the detection function, is the probability of sighting a school that is initially at perpendicular distance x from the track line. The function, $g(x)$, is monotonically decreasing from 1 on the trackline ($g(0) = 1$). Therefore, schools avoiding a ship by effectively moving farther abeam must obtain a value to $g(x)$, say $g(x)^1$, that is less that that at its initial distance x. These reduced values, $g(x)^1$, replace the original values of $g(x)$ at all initial perpendicular distances where avoidance movements began. The area under this altered detection curve (i.e., the plot of $g(x)^1$ against x), which determines the new probability of sighting a school from the track, is accordingly reduced. Reasonable models of the detection function and how it is altered by avoidance behavior can be constructed to show that this reduction can be considerable.

If dolphins do obtain lower $g(x)$ values from their avoidance trajectories, the behavior would be advantageous. This seems entirely possible considering that the schools can cruise at speeds approaching that of many research ships (Table 3) and apparently can detect and continue to sense a ship from considerable distance. Evidence of the latter are the distances at which avoidance behavior was apparent (Table 2) and the near simultaneous changes in school course or speed following course changes by the ship. Such changes occurred at 3.5 mi in school 1, at 6.0 and 3.3 mi in school 2, at 3.2 mi in school 4, and at 2.4 mi in school 7 (Table 1).

With significant reduction in sighting probability possible from avoidance, it would be useful to empirically determine the actual probabilities, $g(x)^1$, or to model this behavior. We expect, however, that the specifics of avoidance trajectories as well as the probabilities would

vary greatly with species, populations and their experience, and the specific behavioral activity of the school when encountered. The type of ship involved and environmental conditions may also affect avoidance behavior.

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THE STRAIT OF GEORGIA HERRING FISHERY: A CASE HISTORY OF TIMELY MANAGEMENT AIDED BY HYDROACOUSTIC SURVEYS

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ABSTRACT

A stock assessment program which combines hydroacoustic biomass estimates with midwater trawl sampling, spawning escapement estimates, and daily catch reporting has provided a timely method of managing an intensively fished, Pacific herring population in Puget Sound, Wash. Since 1976, these techniques have been implemented through the spawning season to estimate adult herring biomass, and to set quotas consistent with the biomass. The estimates become available for management use less than a day following completion of an acoustic-trawl survey, which allows for in-season adjustments in fishing.

Acoustic-trawl surveys carried out at regular intervals during the spawning season monitored declines of prespawning adult herring biomass; the declines corresponded to cumulative increases of catch and spawning escapement. After full recruitment to the fishery, the sum of catch, escapement, and acoustic-trawl estimates provided a point estimate of total available adult herring. Within a season, these point estimates varied less than 15%. This stability is a check on the accuracy of acoustic surveys, and confirms that accuracy is sufficient for management purposes.

Management of virtually all fisheries requires information on the abundance of the resource with which to set catch quotas, limit effort, or determine stock condition. The effectiveness of fishery management is often hampered by the need to make decisions based on stock assessment requiring long time periods or doubtful assumptions, or both.

Fisheries on the west coast of the United States and Canada for sac-roe (egg skein) of Pacific herring, *Clupea harengus pallasi*, have a need for rapid management response. The herring migrate from offshore waters to subtidal and intertidal spawning grounds. The fish are harvested just prior to spawning and the sac-roe is subsequently prepared as a caviar product. Total allowable harvests can be taken in very short times, from minutes to days, and prolonged fishing time easily leads to overharvest. An objective of sac-roe herring management is to obtain real time estimates of abundance prior to and during the fishery so that quotas compatible with abundance may be established. Spawning escapement goals must be met without losing the opportunity to catch harvestable fish.

Traditional methods of determining abundance or setting fishing rates are inadequate for the short-duration sac-roe herring fisheries. Catch per unit effort (CPUE), virtual population analysis/cohort analysis (VPA), or yield per recruit (Y/R) provide postharvest information, and often with lags of several years. Problems with effort standardization and harvesting aggregated fish (CPUE), the need for independent estimates of highly variable recruitment (VPA), and sexual maturity being reached after maximum cohort biomass (Y/R) make these methods difficult to apply to in-season sac-roe herring management even without the timeliness factor.

Sac-roe herring management relies heavily on catch records and on spawning escapement estimates. Even though these values ultimately combine to estimate total abundance, they are too late for in-season estimates and in-season management modifications. Abundance estimates before and during the spawning/fishing season can be obtained by use of hydroacoustic techniques, as are used in Washington, Alaska, and British Columbia.

Successful management of the sac-roe herring fishery in the Strait of Georgia, Wash., requires timely information on the abundance of the fishable stock during the fishing season. A fleet composed of purse seiners and gill netters has the capacity to harvest the available quota within 1

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to several days. In addition, allocation to treaty Indian fishermen is required by Federal Court rulings (the Boldt decision), which established separate treaty and nontreaty quotas. Biologists representing Washington State, participating tribes, and the University of Washington agreed that a target quota should be 20% of the total estimated population biomass (Trumble 1980).

The application of hydroacoustic techniques offered timeliness in the Strait of Georgia herring stock assessment program (Thorne 1977a) when combined with midwater trawling, analysis of catch records, and spawning ground surveys. This paper presents results of application of these techniques during 1976-79 to the management of the fishery.

METHODS AND MATERIALS

The concept of the sac-roe herring stock assessment program is to estimate the biomass of adult herring in prespawning condition, and add to this the biomass of adult herring removed by spawning or being caught. Hydroacoustics provided estimates of total pelagic fish biomass, and midwater trawl sampling provided species composition data to identify prespawning adults; the combination of hydroacoustics and midwater trawling will be referred to as "acoustic-trawl." Spawning ground surveys provided estimates of spawning escapement, and catch records tracked the success of the fishery. Catch and escapement estimates provide a postfishery check on the accuracy of the acoustic data, and in conjunction with acoustic-trawl surveys, a series of in-season estimates of the total biomass of mature herring.

Acoustic Survey Equipment and Methods

The hydroacoustic data acquisition system consisted of a modified 105 kHz Ross[3] 200A echosounder, an interface amplifier that reduced the signal frequency from 105 kHz to 5 kHz, a Sony TC-377 tape deck which recorded the 5 kHz data on magnetic tape, and an oscilloscope to monitor system operation. The transducer produced a 7½ degree full angle beam at the half power (−3dB) points. The modifications of the system include an internal calibration oscillator to monitor and measure system gain (Thorne et al. 1972; Nunnallee 1973). The echosounder transmitted a pulse length of 0.6 m s. The echosounder and transducer were periodically calibrated at the Applied Physics Laboratory, University of Washington. Normally, calibration occurred at the beginning and end of each field season.

The acoustic data from the magnetic tapes was processed with a digital echo integration system implemented on a PDP 11/45 computer (Thorne 1977b). A mean target strength of −33 dB/kg was used by the program to scale the integrator data to estimates of fish density. This value was originally established on the basis of both comparisons with net tows and in situ target strength measurements (Thorne 1977a) and the value still appears to be reasonable. Although considerable information has been obtained on the dependence of target strength on fish length (FAO 1978; Thorne in press), the variation in mean fish lengths in the Strait of Georgia is insufficient to warrant using a length-dependent variable instead of a constant for the target strength scaling factor. Herring typically range from 18 to 24 cm SL, and compose 70-90% of the biomass in the acoustic-trawl surveys.

During 1976 and 1977, the University of Washington's 12 m RV *Malka* was used as the acoustic platform, with a hull-mounted transducer. Subsequently, the acoustic program chartered a 10 m gill net vessel and used an over-the-side pole-mount for the transducer.

Acoustic surveys were conducted during April and May (and to the first part of June 1976) in order to bracket the spawning migration of the herring (Lemberg 1978). The surveys were conducted between Point Roberts and Lummi Island on a standardized trackline which had 10 transects, each about 8 km in length (Fig. 1). The surveys were typically conducted at twice weekly intervals around the peak of the migration, and less frequently during the early and late stages of the run.

During the day, herring normally aggregate in tight schools at depths of 40 m or more. At night, the schools disperse and form widespread layers 5-10 m thick at depths of 10-30 m; herring density decreases such that many fish are distinguishable as individual targets. Until actively ready to spawn, herring remain in water deeper than 20 m. The survey area encompassed the prespawning holding area, bounded by the 8-10 fathom contours on the inside, and the 50-60

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

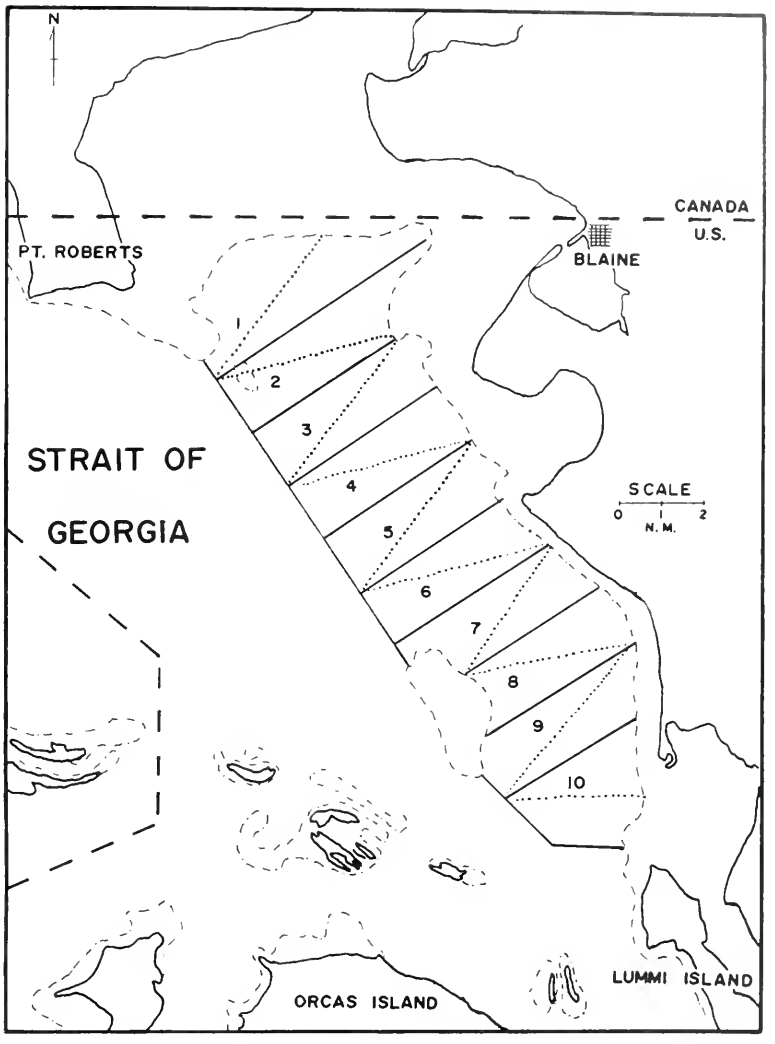

FIGURE 1.—Strait of Georgia standard track line pattern (....). Solid lines and 10-fathom contour (-·-) define survey subareas (from Lemberg 1978).

fathom contours on the outside. Spawning occurs on adjacent shorelines.

The surveys were conducted at night when the herring were less patchily distributed and further off bottom. Transects were evenly spaced and designed for maximum mileage during hours of darkness. At about 0.5 h per transect, plus turn around and set up time between transects, each survey required the approximately 6 h of darkness.

Data were integrated for density (kg/m^3) at preselected depth intervals for each transect; depth interval densities were accumulated for a depth zone, usually 5-40 m below the surface to calculate an average density (kg/m^2) for each transect. Extrapolation of average density to the surface area represented by each transect, summed over all transects, provided biomass estimates. The acoustic estimates of maturing adult herring biomass were available the afternoon following each survey.

Midwater Trawling Procedures

The midwater trawl sampling was done from chartered 20-24 m commercial fishing trawlers simultaneously with the acoustic surveys. This procedure has two advantages in addition to synopticity. First, the vessel requirements for the acoustic vessel are less demanding so that a smaller, less expensive vessel could be used. Second, it was possible to direct the towing

operation from the acoustic vessel on the basis of target abundance from the echograms in an attempt to approximate optimal sampling allocation (Cochran 1977).

The net employed was a four panel midwater trawl with 9.2 m headrope and footrope and 9.2 m sides designed to open 6.1 m vertically and horizontally; meshes tapered from a 7.6 cm stretch mesh in the wings to a 1.27 cm stretch mesh cod end liner. Head rope floats and chain on the foot rope were used to aid the vertical opening. Trawl doors were metal, V-type, and weighed 31 kg; 55 m dandylines extended from the doors to the side panels. Trawl depth was monitored with a bathykymograph and in 1977, by third wire telemetry to one of the trawl doors.

A typical survey included three to five 30-60 min tows. The number of tows was limited by hours of darkness. Catches were sorted on board by major species, normally herring, dogfish, cod, and smelt, and by incidentals; each species aggregate was weighed separately. Two subsamples of herring were collected from each tow. One subsample was processed on board to determine maturity (prespawning, spent, and immature). The other was returned to the laboratory for length, weight, age, sex, and sexual maturity data.

Spawning Ground Surveys

The herring lay adhesive eggs on lower intertidal and upper subtidal vegetation. The biomass of herring which have spawned can be estimated from the intensity and extent of spawn deposition in conjunction with fecundity, sex ratio, and average weight data (Hourston et al. 1972). The basic procedure is to sample vegetation along the shoreline and note the intensity (number of egg layers) of deposition. A spawning ground survey crew used a small (4-5 m) boat with outboard motor to maneuver nearshore, and a grappling rake to retrieve vegetation at 350-500 m spacing along the spawning grounds. Observations on spawning intensity and extent are then converted to an estimate of the spawning escapement (Trumble et al. 1977; Meyer and Adair 1978). The survey intensity during the spawning period is typically twice weekly for each of four major spawning areas in the Strait of Georgia. During the 2-mo period (April-May) that encompasses the extremes of the spawning period, 15-20 spawning ground surveys are conducted for each of the four areas. The objective to maximize number of surveys to reduce the time between spawn deposition and survey is limited by available personnel.

Catch Records

The Washington Department of Fisheries has a computerized data retrieval system for preliminary catch statistics. Telephone reports of daily estimated catch (soft data) are required from each buyer by noon of the day following the catch. These telephone reports are replaced and updated when fish receiving tickets (hard data) arrive. Management during the fishery used both soft and hard data; this report used final data. Summary reports of daily and cumulative landings by treaty and nontreaty fishermen, and totals for the combined fleet, are available through the catch data retrieval system.

RESULTS

A point estimate of sac-roe herring abundance was made the day following each hydroacoustic survey by incorporating cumulative spawning escapement estimates and cumulative catch up through the date of each hydroacoustic survey. This procedure assumed that acoustic-trawl estimates represent maturing adult fish remaining to spawn, while cumulative catch and escapement account for adult fish removed from the spawning population. The point estimates should be similar once the stock has fully recruited to the area, and will then represent total biomass; as acoustic estimates decline through the season, compensating increases in catch and escapement occur.

1976 Surveys

The total acoustic biomass estimates in the study area during 1976 ranged from an initial value of 1,920 tons 5-8 April to a peak of 21,000 tons on 21-22 April (Table 1). Trawl catches were predominately herring (about 90% by weight). However, a large proportion of the herring biomass was often either juvenile or spawned out fish. Only 58% of the total biomass estimates was maturing herring at the time of the peak estimate. The acoustic-trawl estimates of maturing herring increased from 1,480 tons during the first survey on 5-6 April to a maximum of 12,240 on 21-22 April, and decreased to 0 tons on the last survey, 3-4 June (Fig. 2).

TABLE 1.—Results from hydroacoustic-midwater trawl surveys in the Strait of Georgia, Wash. (weights in short tons), 1976.

Date	Total	Maturing adult herring	Juvenile or spent herring	Miscellaneous	% spawners
4/5-6	1,920	1,480	440	—	77.1
4/13-14	7,030	4,030	2,150	850	57.3
4/21-22	21,100	12,240	6,360	2,500	58.0
4/27-28	10,940	8,370	1,400	1,170	76.5
5/5-6	7,050	3,460	2,170	1,420	49.1
5/19-20	4,530	1,460	1,830	1,240	32.2
6/3-4	2,090	0	990	1,100	0

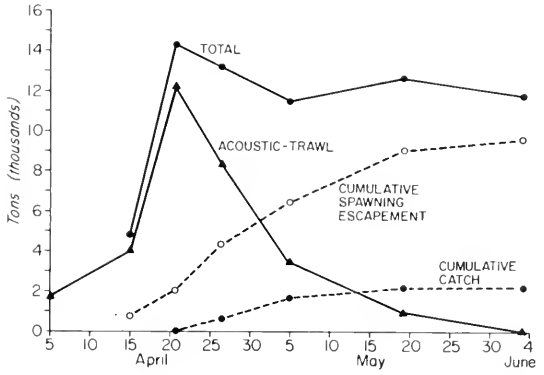

FIGURE 2.—Biomass estimates of adult roe-herring in the Strait of Georgia, 1976.

Fifty-nine spawning ground surveys were conducted between 8 April and 8 June. The total spawning biomass from these surveys was estimated to be 9,590 tons (Fig. 2). The fishery extended from 25 April to 23 May with a total catch of 2,190 tons.

The highest point estimate of total adult herring biomass, on 21-22 April, was slightly over 14,000 tons and was predominately from the acoustic-trawling data. The last estimate, 11,800 tons, was from the spawning escapement estimate plus the total catch. The average of the five estimates between 21-22 April and 3-4 June was 12,700 tons. The fishery harvested 17.4% of the maturing adult biomass, well within the 20% limit.

1977 Surveys

Fish abundance in the study area in 1977 followed the general pattern of 1976, building up to a peak and then declining as the herring moved inshore to spawn. The total acoustic biomass estimates in the study area ranged from a peak value of 10,090 tons on 25-26 April to a minimum value of 3,410 tons on 17-18 May (Table 2). The trawl catches were again predominately herring. The proportion of maturing adult herring ranged from 69% to 84% of the total catch during the first half of the survey period when the acoustic-trawl estimate composed the major component of the total biomass; later in the season proportions decreased. The acoustic-trawling estimate of spawner herring reached a peak of 7,900 tons (Fig. 3).

Seventy-seven spawning ground surveys were conducted from 7 April to 9 June. The estimated spawning escapement was 8,800 tons (Fig. 3). The fishery extended from 11 April to 12 May with a total catch of 2,300 tons.

The timing of the migration differed slightly from 1976. Significant amounts of spawning and substantial catches occurred before the peak of the acoustically measured biomass. Consequently, the first total biomass point estimate after presumably full recruitment, 11,300 tons, included substantial inputs from the spawning ground surveys and catch data, as well as the acoustic (Fig. 3). The last estimate was 11,100 tons, composed of the 8,800 ton spawning escapement estimate and the 2,300 ton catch. The mean of the final catch plus escapement and the five surveys from presumably full recruitment was 11,040 tons. The harvest rate reached 20.8% for 1977.

TABLE 2.—Results from hydroacoustic-midwater trawl surveys in the Strait of Georgia, Wash. (weights in short tons), 1977.

Date	Total	Maturing adult herring	Juvenile or spent herring	Miscellaneous	% spawners
4/5-6	4,530	3,130	1,210	190	69.1
4/12-13	4,340	2,990	1,060	290	68.9
4/18-19	7,480	6,280	710	490	83.9
4/21-22	7,700	5,770	1,230	700	74.9
4/25-26	10,090	7,900	1,430	760	78.3
4/28-29	8,950	5,000	3,160	790	55.9
5/3-4	9,600	4,260	1,610	3,730	44.4
5/10-11	3,560	2,060	1,070	430	57.9
5/17-18	3,410	550	1,960	900	16.1

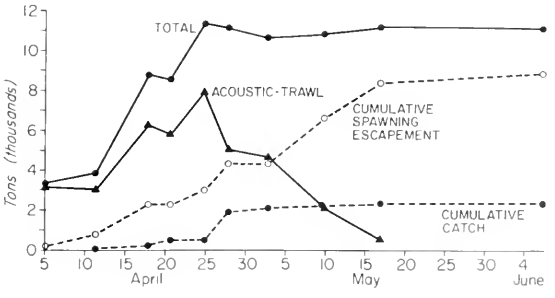

FIGURE 3.—Biomass estimates of adult roe-herring in the Strait of Georgia, 1977.

1978 Surveys

Herring abundance estimated through the 1978 season showed considerably more variability than in other years of the surveys (Fig. 4, Table 3). As expected, abundance was low at the time (11-12 April) of the first acoustic-trawl survey. The following week, 16-22 April, acoustic-trawl estimates of maturing adult herring increased to approximately 13,400 tons in each of two surveys, and the total estimate exceeded 16,000 tons. For the next three surveys, 24 April-1 May, acoustic-trawl estimates of maturing adult herring biomass in the survey corridor dropped considerably, and corresponding total abundance declined to 10,000-11,000 tons. On 4-5 and 8-9 May estimates of total maturing herring increased to 13,000 tons; these latter estimates included 3,500-6,000 tons from acoustic surveys.

The highest biomass estimate occurred just after complete immigration when the estimate comprised mostly acoustic data. The original high values, midseason low values, and intermediate values at the end of the season were composed of at least two similar estimates, which suggests that the changes represent actual occurrences.

The final spawning escapement estimate, based on 67 spawning ground surveys was 8,840 tons. Total catch was 2,120 tons. Cumulative escapement plus catch equaled 10,960 tons. Mean value of the eight population estimates made from the time of completed immigration to the survey area was 12,700 tons. The 16.7% harvest rate, lowest of this 4-yr series, was due to a reduced quota during the midseason period of low abundance estimates.

TABLE 3.—Results from hydroacoustic-midwater trawl surveys in the Strait of Georgia, Wash. (weights in short tons), 1978.

Date	Total	Maturing adult herring	Juvenile or spent herring	Miscellaneous	% spawners
4/11-12	6,340	5,450	700	190	86.0
4/17-18	17,420	13,450	2,540	1,430	77.2
4/20-21	17,420	13,410	3,670	340	77.0
4/24-25	9,100	6,380	1,850	870	70.1
4/26-27	8,820	6,250	1,870	700	70.9
5/1-2	7,310	4,350	1,930	1,030	59.5
5/4-5	9,700	5,960	2,780	960	61.4
5/8-9	6,400	3,650	2,330	420	57.0

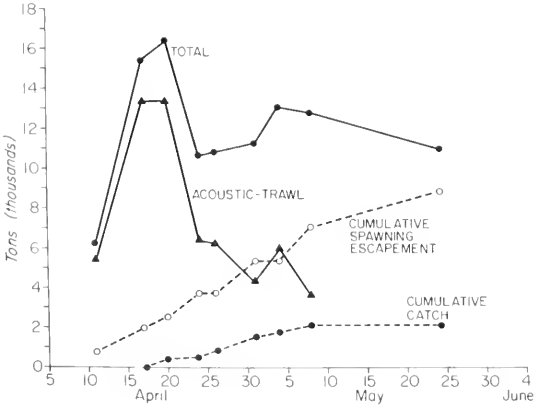

FIGURE 4.—Biomass estimates of adult roe-herring in the Strait of Georgia, 1978.

1979 Surveys

Total all-species acoustic abundance estimates (Table 4) increased from a normal low value of about 3,000 tons in mid-April to a peak of 8,150 tons following presumed full recruitment on 27 April. By the end of the season, estimates were less than 3,000 tons. Maturing adult herring comprised 50-70% of acoustic biomass until the last survey of the season. Early season estimates of 1,000-2,000 tons of adult herring increased to about 5,600 at the peak, and declined to 890 tons on 7-8 May.

Seventy-two spawning ground surveys conducted during 1979 provided an escapement estimate of 8,040 tons. Total harvest was 1,920 tons.

Variation in 1979 seasonal abundance estimates for adult (spawner) herring showed a pattern similar to those observed in 1976 and 1977: biomass increased rapidly early in the season, and remained fairly constant for the duration of sampling (Fig. 5). From the time of full recruitment, total adult herring estimates ranged from 8,000 to 10,000 tons. As in 1977, considerable spawning and catch occurred prior to the peak acoustic estimate, and added considerably to the first estimate following presumed full

TABLE 4.—Results from hydroacoustic-midwater trawl surveys in the Strait of Georgia, Wash. (weights in short tons), 1979.

Date	Total	Maturing adult herring	Juvenile or spent herring	Miscellaneous	% spawners
4/11-12	3,840	2,340	1,460	40	60.9
4/16-17	2,680	1,290	1,370	20	48.1
4/19-20	4,410	2,580	1,530	300	58.5
4/23-24	5,270	3,330	1,730	210	63.2
4/26-27	8,150	5,590	2,200	360	68.6
4/30-5/1	5,750	4,110	1,520	120	71.5
5/3-4	2,510	1,390	1,080	40	55.4
5/7-8	2,870	890	820	1,160	31.0

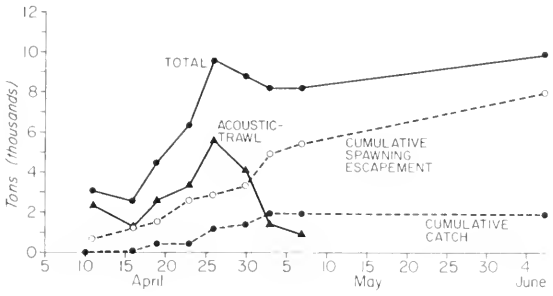

FIGURE 5.—Biomass estimates of adult roe-herring in the Strait of Georgia, 1979.

recruitment. Average estimate of total adult herring biomass was 8,950 tons. The fishery harvested 21.8% of this estimated biomass in 1979.

DISCUSSION AND CONCLUSIONS

The combination of techniques applied in the management of the sac-roe herring fishery provides a timeliness and accuracy greater than any single technique. The catch records are obtained rapidly, but by themselves have little management value. CPUE data are difficult to evaluate in a timely manner and has questionable application in a mixed gill net and purse seine fishery on schooling fishes whose migration patterns and timing vary annually; consequently, CPUE data are not used in the sac-roe herring fishery. The spawning ground surveys provide escapement data, but are not timely for in-season management of the fishery. Conceivably the excess biomass could be harvested after escapement goals have been met, but this approach forces the fishery to the end of the season when fish are younger, smaller, and less valuable than early in the season.

The hydroacoustic-trawling data provide the single most useful information for in-season management. The estimates of potential spawning biomass are available for management decisions by the end of the day following the nighttime survey. The acoustic-trawl data have provided good agreement with the other measure of biomass. The average of the weekly total run size estimates from the sum of all three data sources have varied from 1% to 14% of the final estimate from the catch and spawner escapement estimate (Table 5).

In all 4 yr the peak acoustic-trawling estimate in conjunction with these data has provided a

TABLE 5.—Stock assessment summary, U.S. Strait of Georgia sac-roe herring, 1976-79.

Year	Total catch	Total escapement	Catch + escapement	Average of full recruitment point estimates[1]
1976	2,190	9,590	11,780	12,700
1977	2,300	8,800	11,100	11,040
1978	2,120	8,840	10,960	12,700
1979	1,920	8,040	9,960	8,950

[1]This estimate consists of the average of acoustic-trawl plus cumulative escapement plus cumulative catch point estimates from the time of full recruitment through the final catch plus escapement estimate.

reasonable and timely estimate of total run size. However, the estimate of total run size obtained using the peak acoustic-trawl estimate was higher than the final estimate for all years except 1979, and higher than all in-season point estimates. Variability (random or unsystematic factors) may contribute to the result, but in general the high sampling power of acoustics and the fairly uniform distribution of the herring render this component inconsequential (Saville 1977), and 95% confidence intervals calculated from the acoustic data are typically on the order of ±10%. Variability associated with the trawling data for species composition is probably more important, but is difficult to incorporate. Combined acoustic-trawling variance estimation procedures have been developed for other studies (Thomas 1979; Thomas et al. 1979); however, they were not applied in this study since we were more concerned with the sources of potential error (systematic factors or bias). Three sources of bias may contribute to the observed differences between the peak acoustic-trawling estimate and the final estimate. The acoustic estimates may be biased high because of the target strength assumption, but the acoustic techniques may underestimate later in the run when the fish move into shallow water just prior to spawning. Studies by other investigators indicate that a value of −32 dB/kg (which would result in a 20% lower estimate) may be more reasonable (Nakken and Olsen 1977; FAO 1978) than the −33 dB/kg value used. Alternatively, the estimates from spawning ground data could be biased to the low side.

Clearly more information on target strength is needed to confidently establish the accuracy of the acoustic technique as a measure of fish biomass. The reasonable agreement with the sum of the spawning escapement estimates and catch is reassuring, but the spawning escapement estimates are also subject to bias and uncertainty, and the exploitation rate has been too consistent to give much insight into the magni-

tude and direction of potential bias in these two estimators.

In spite of the present uncertainties in the accuracy of both the spawning escapement and the acoustic-trawl estimates, the results are well suited to the current management plan of the fishery. The objective of present management procedures is to maintain the population at recent historical levels through a combination of a biologically reasonable exploitation rate and a minimum escapement level. The accuracy of the acoustic techniques probably already exceeds our understanding of optimal exploitation rates. Thus, while improvements are conceivable and may be dictated by future developments in the fishery, the present procedures provide a sound interim approach with timeliness which has been rarely achieved in fishery management.

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NOTES

EFFECTS OF LONG-TERM MERCURY EXPOSURE ON HEMATOLOGY OF STRIPED BASS, *MORONE SAXATILIS*

The striped bass, *Morone saxatilis*, is found along the shore of the heavily populated Atlantic coast of North America; hence, it is subjected to considerable domestic and industrial pollution. Even higher pollutant concentrations may be encountered when the fish migrate into rivers to spawn. Because of the availability of the species, its value to both commercial and sport fisheries, and its normal habitat in many areas where pollution is a problem, the striped bass may be a particularly appropriate indicator species for pollution studies. In spite of these factors, information about sublethal effects of metal on striped bass is limited; even the response of the species to mercury, perhaps the most widely studied heavy metal, has received little attention in the literature.

That fish accumulate mercury from water has been demonstrated both in the laboratory and in the wild. Pentreath (1976), in a study of accumulation, distribution, and retention of mercury, found a gradual uptake and slow loss of ^{203}mercury in the plaice, *Pleuronectes platessa*, during laboratory exposures up to 90 d. Olson et al. (1973) showed that the rainbow trout, *Salmo gairdneri*, accumulates mercury through the gills. Our laboratory demonstrated uptake of mercury into the winter flounder, *Pseudopleuronectes americanus*, during a 60-d laboratory exposure (Calabrese et al. 1975). Mercury analyses on fish taken from their natural environment corroborate the laboratory findings: An increasing mercury concentration correlated with increasing weight has been demonstrated in the pike, *Esox lucius*; the bluefish, *Pomatomus saltatrix*; the blue hake, *Antimora rostrata*; and the striped bass (Johnels et al. 1967; Alexander et al. 1973; Cross et al. 1973).

The sensitivity of striped bass to pollution in general has been reported by a number of investigators. Raney (1952) noted that, although the striped bass had formerly used as spawning areas most of the large rivers along the Atlantic coast of the United States, the species had virtually disappeared from many of these areas, notably the Delaware, Connecticut, and Roanoke Rivers; he attributed its disappearance to gross pollution. Chittenden (1971) also attributed the lack of striped bass in the Delaware River to gross pollution and suggested that a major limiting factor was the river's very low oxygen content. An earlier study in our laboratory demonstrated sublethal responses of the striped bass to mercury. Juvenile striped bass were exposed to 5 and 10 parts per billion (ppb) mercury for periods ranging from 30 to 120 d. Measurements of gill-tissue oxygen consumption showed changes whose magnitude and direction varied with length of exposure (Dawson et al. 1977).

The present study was undertaken to determine the nature and extent of physiological disturbance to striped bass caused by mercury exposure using a variety of hematological tests. Variables related to the oxygen-carrying capacity of the blood, such as hemoglobin and hematocrit, were considered important because of earlier indications that mercury exposure affects respiration (Dawson et al. 1977), because of the suggestion that low oxygen levels eliminate striped bass from certain polluted environments (Chittenden 1971), and because of evidence that mercury affects these measurements in other fish (Calabrese et al. 1975; Dawson 1979). In addition, because my earlier work indicated that mercury disrupts osmo- and ion-regulation in winter flounder (Dawson 1979), I included these aspects of plasma chemistry in the present study.

Methods

Exposure

Striped bass were obtained from the Edenton National Fish Hatchery, U.S. Fish and Wildlife Service, Edenton, N.C., where they had been reared in freshwater. Upon arrival at the Northeast Fisheries Center Milford Laboratory, they were placed directly into flowing Milford Harbor seawater and allowed to acclimate for 2 wk prior to exposure. Throughout the acclimation and the exposure period the fish were fed Purina Trout Chow[1] ad libitum, daily. The fish

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

were exposed in 80 l glass aquaria filled to 60 l with sand-filtered seawater by a proportional-dilution apparatus (Mount and Brungs 1967). The dilutor controlled the intermittent delivery of mercury-treated and control water at a flow rate of 1 l to each tank every 3 min throughout the test period. This provided a flow of 480 l/tank per d and an estimated 90% replacement time of 7 h (Sprague 1969). Mercury, as mercuric chloride, was added at concentrations of 5 and 10 ppb. The concentrations are nominal concentrations of the metal ion in solution, not including the background level, which was below 0.3 ppb. The fish were exposed for 60 d and then removed for testing. Each tank contained 5 fish, for a total of 15 fish at each mercury concentration and 15 controls. The fish averaged 17.1 cm long (range 13.1-19.0) and 59.3 g (range 22.7-79.3). The exposure ran from late November 1976 to January 1977. The temperature ranged from a high of 8°C at the beginning of the exposure period to a low of 0°C at the termination of the exposure. Salinity during the exposure period averaged 27.0‰ and ranged from 26.0 to 29.6‰ with the exception of 1 d when it fell to 20‰.

Hematology

Blood was collected from each fish by cardiac puncture using a 3 ml plastic syringe and a 22-gage needle. The sample was transferred gently into an 8 ml glass vial containing 150 units of dried ammonium heparinate as an anticoagulant. Microhematocrits (packed red cell volumes) were determined following centrifugation for 5 min at 13,500 × *g*. Hemoglobin concentrations were determined by the cyanmethemoglobin method using the Hycel reagent; absorbance was read on a Bausch and Lomb Spectronic 20 spectrophotometer at 540 nm. Erythrocytes were counted in a hemacytometer using Natt-Herricks diluting fluid (Natt and Herrick 1952) at a 1:200 dilution. Within 4 h after collection, the remaining blood sample was centrifuged at 12,000 × *g* for 4 min and the plasma frozen for later determination of osmolality, protein, sodium, potassium, and calcium. Plasma sodium, potassium, and calcium concentrations were measured with a Coleman 51 flame photometer. Plasma protein was determined by the Biuret method as modified by Layne (1957). Plasma osmolalities were determined on an Advanced 3L osmometer using a 0.2 ml sample. Samples were pooled as necessary to obtain a 0.2 ml volume. The effect of the added heparin on the osmolality was negiligible. Three indices were computed from the measured values: mean corpuscular volume in cubic micrometers/cell = Hct/RBC × 10, mean corpuscular hemoglobin in picograms/cell = Hb/RBC × 10, and mean corpuscular hemoglobin concentration in grams/100 ml packed red cells = Hb/Hct × 100. All data were analyzed using Student's *t*-test.

Results

Control fish had a mean hematocrit of 47%, a hemoglobin concentration of 8.7 g/100 ml, and a red cell count of 4.10×10^6 cells/mm^3 (Table 1). These values resemble those reported by other investigators: Courtois (1976), using striped bass of similar size acclimated to cold seawater, reported a mean hematocrit of 46 and a hemoglobin of 8.4. More recently, Westin (1978) reported a hematocrit of 47.9, a hemoglobin of 9.11, and a red cell count of 3.79 for adult striped bass during the spawning season.

The effects of mercury on the erythrocyte component of the blood were pronounced (Table 1). Hematocrit, hemoglobin, and RBC all decreased following mercury exposure. In each case the response was significantly greater at the higher mercury concentration. The reduction in hemoglobin was proportional to the reduction in red cell count: About 10% in the 5 ppb-exposed animals and about 25% in the 10 ppb-exposed animals. This is reflected in the lack of change of the mean corpuscular hemoglobin and indicates that the lowered hemoglobin concentration in exposed fish is the result of a lower number of circulating erythrocytes and not of a smaller quantity of hemoglobin in each cell. The de-

TABLE 1.—Effects of 60-d exposure to mercuric chloride on erythrocytes of striped bass (means ± SE with ranges in parentheses).

Test	Controls	5 ppb	10 ppb
Hematocrit, % packed cells	47±1.3 (38-56)	36±1.2** (30-47)	26±1.6** (17-36)
Hemoglobin, g/100 ml whole blood	8.7±0.05 (7.8-9.9)	7.8±0.13** (7.2-8.9)	6.6±0.32** (4.9-8.8)
Red blood cells, 10^6 cells/mm^3	4.10±0.106 (3.69-4.81)	3.82±0.106 (3.19-4.45)	3.03±0.180** (2.10-4.57)
Mean corpuscular volume, μm^3/cell	115.2±3.70 (96-147)	96.6±3.69* (69-118)	86.2±3.58** (65-114)
Mean corpuscular hemoglobin, pg/cell	21.4±0.52 (18.5-25.9)	20.3±0.54 (16.6-23.4)	21.9±0.73 (18.7-29.0)
Mean corpuscular Hb concentration, g/100 ml packed red cells	18.7±0.44 (17.0-21.6)	21.8±0.57** (18.9-27.3)	25.6±0.58** (22.8-28.8)
Number of samples	14	15	13

*Significantly different from controls at 0.005 level, **Significantly different from controls at 0.001 level.

creases in hematocrit were greater proportionately: 23% and 45% of the control value in the 5 and 10 ppb-exposed groups. The greater decrease in hematocrit represents not only a lower number of red cells but, in addition, a smaller mean volume in red cells of exposed animals, reflected in the significantly lower mean corpuscular volume for exposed animals.

Exposure to mercury also affected the osmo- and ion-regulatory capacity of the striped bass (Table 2). There was no significant difference between 5 ppb-exposed fish and controls in any of the five plasma chemistry variables measured. In the 10 ppb-exposed animals, the plasma sodium and the osmolality increased to 238 mEq/l and 462 mOsm. Plasma calcium dropped to 3.98 mEq/l in the 10 ppb-exposed group, significantly lower than the control value of 4.52. Although the mean calcium concentration in the 5 ppb-exposed fish was even lower, because of the greater variability in that group, it was not significantly different from that of controls. There was no significant difference between controls and 10-ppb-exposed fish in plasma protein or potassium.

TABLE 2.—Effects of 60-d exposure to mercuric chloride on plasma chemistry of striped bass (means ± SE with ranges in parentheses). Plasma samples were pooled as necessary to obtain volume of material required.

Test	Controls	5 ppb	10 ppb
Na, mEq/l	195±2.6 (180-202)	198±2.1 (174-204)	238±6.2** (210-262)
K, mEq/l	6.57±0.799 (3.00-9.60)	5.19±1.088 (2.20-9.80)	5.00±0.588 (2.40-9.00)
Ca, mEq/l	4.52±0.135 (4.00-5.30)	3.90±0.303 (2.98-5.80)	3.98±0.146* (3.26-4.74)
Protein, g/100 ml	3.70±0.218 (3.14-4.58)	3.51±0.016 (3.05-4.15)	3.34±0.446 (2.38-5.18)
Osmolality, mOsm	354±10.8 (321-395)	369±6.9 (346-398)	462±11.8** (435-519)
Number of samples	8	8	10

*Significantly different from controls at 0.05 level, **Significantly different from controls at 0.001 level.

Discussion

Mercury had a major disruptive influence on the hematology of the striped bass, affecting both the red cell component of the blood and the plasma chemistry. Mercury had similar effects on winter flounder in an earlier study (Dawson 1979). In general, the changes demonstrated in winter flounder paralleled those of striped bass although the magnitude of change was smaller in the winter flounder in spite of higher mercury concentrations, namely, 10 and 20 ppb. The one exception was that the mean corpuscular volume increased in winter flounder and decreased in striped bass. The greater sensitivity to mercury in striped bass may represent a real species difference or may simply reflect the smaller size of the striped bass used.

The alterations in plasma sodium and osmolality following mercury exposure may be caused by gill-tissue damage. Meyer (1952) found decreased uptake and increased loss of sodium in the gills of mercury-exposed goldfish in freshwater. Olson et al. (1973) found ultrastructural damage in rainbow trout gills following mercury exposure. Renfro et al. (1974) demonstrated mercury uptake by the gill of the killifish, *Fundulus heteroclitus*, in freshwater and concomitant inhibition of sodium uptake. Our laboratory has demonstrated mercury uptake from seawater into the gills of winter flounder (Calabrese et al. 1975).

At least two sites of mercury accumulation have been described which could account for changes in the red cell component of the blood. Olson et al. (1973) and Pentreath (1976) reported the uptake of mercury into the blood of rainbow trout and plaice which could lead to direct cell damage. Perhaps more relevant are reports of mercury accumulation in the kidneys of teleosts; this would very likely affect renal hemopoiesis and, hence, such variables as hematocrit, hemoglobin, and RBC. Olson et al. (1973) reported a high mercury concentration in the kidney rainbow trout following a 24-h exposure. Pentreath (1976) reported that, following a 60-d exposure of the plaice to ^{203}Hg, the kidney was among the organs highest in ^{203}Hg.

Hematology is a valuable tool for assessing a variety of stresses in fish. Its main limitation lies in the lack of information about the normal range of values in fish. Wedemeyer and Yasutake (1977) have noted that, in general, hematological measurements show a greater variation in fish than in many other animals. Fish are subjected to a wide range of temperature, salinity, and nutrient availability, all of which are likely to be reflected in their hematology. Courtois (1976) has demonstrated hematological changes in striped bass exposed to varying conditions of temperature and salinity. Bridges et al. (1976) have demonstrated significant seasonal variation in winter flounder hematology. Hesser (1960), Blaxhall and Daisley (1973), and Wedemeyer and Yasutake (1977) have attempted to standardize and interpret

hematological tests as applied to fish. The gradual accumulation of the necessary background information should make fish hematology an even more useful tool in the future.

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RAPID AND SPONTANEOUS MATURATION, OVULATION, AND SPAWNING OF OVA BY NEWLY CAPTURED SKIPJACK TUNA, *KATSUWONUS PELAMIS*

This study was designed to test a hypothesis, formulated on the basis of preliminary observations, that skipjack tuna, *Katsuwonus pelamis*, captured in Hawaiian waters during their breeding season and maintained alive would ovulate spontaneously within a few hours after capture. If such did occur, and on a consistent and predictable basis, this would be of practical value in attempts to spawn these fish in captivity.

Methods

These investigations took place at the Kewalo Research Facility of the National Marine Fisheries Service Honolulu Laboratory. Six deliveries of live skipjack tuna were received from two commercial fishing vessels during June and July 1980, within the normal spawning season of the species in Hawaiian waters (Brock 1954; Matsumoto 1966). The fish had been caught by standard pole-and-line methods and transported to the receiving dock of the laboratory in baitwells. Upon delivery they were transferred to circular tanks, 7.3 m diameter by 1.1 m deep, provided with continuous flow of seawater. Time of capture for all groups was between 1500 and 1700; time elapsed between capture and delivery to the laboratory ranged from 3.5 to 8 h, with a mean of 5.5 h. Sea temperatures at the capture sites were not measured, but were probably between 25° and 30°C. Water temperatures in the holding tanks were about 25° to 26°C. With all except the first group, a siphon and straining net were used to sample water continuously from the holding tanks to detect the release of their slightly buoyant, pelagic ova. For the last four of the six groups, we arranged also to receive specimens fished from the same school but refrigerated on ice immediately after capture. All the specimens were between 40 and 50 cm in fork length (FL) and 1.4 to 2.2 kg; tunas larger than this are difficult to keep alive in the baitwells of these vessels (about 145 by 165 by 130 cm deep on the vessel which delivered five of the six groups). Skipjack tuna of this size are between 1 and 2 yr old and are probably in their first spawning season (Brock 1954; Yoshida 1971).

We determined gonadal maturation states of specimens at various specified times following their capture, either through biopsies on live specimens or through postmortem dissections. Unless a specimen is already running ripe, neither its sex nor gonadal maturity can be determined through external appearances. Biopsies involved extraction of gonadal tissue by catheterization through the urogenital pore of restrained, unanesthetized fish. Ova were teased free from unpreserved, fresh or refrigerated ovarian tissue, immersed in a 0.9% saline solution, and the diameters of 25 from each of the largest and second largest developing groups were measured with an ocular micrometer. Also, since we were interested primarily in the occurrence and progress of ovulation, we classified females into the following four categories: Unovulated—ripe ova not present in ovarian lumen, developing ova enclosed within follicles; ovulating—some ripe ova present in ovarian lumen but not easily stripped from females, follicles contain large, preovulatory ova 0.80 to 1.0 mm in diameter; ripe—ovarian lumen filled with large quantities of ova which can be easily stripped from females; spent—few residual ova present in ovarian lumen, follicles with relatively small ova of <0.5 mm diameter.

Results

Responses of each sex remained constant among the six groups. Testes of males sacrificed after 7 to 8.5 h appeared identical to those sacrificed and refrigerated on capture. All males had testes that were mature, white, and firm and had thick, viscous milt in the sperm ducts. None yielded milt when moderate stripping pressure was applied. To fertilize ova stripped from females, we had to squeeze milt directly from testes dissected from sacrificed males.

Observations on all six groups of female skipjack tuna received from 8 June to 31 July are summarized in Table 1. None of the 16 specimens killed and refrigerated on capture was in an ovulatory state. The maturing ova in the largest modal group averaged 0.59 to 0.64 mm in 14 of these females and 0.74 mm in another, while the remaining individual had relatively immature ovaries (Table 2). Nine females which died in transit to the laboratory were placed in refrigeration. Times of death had not been recorded by the fishing crews, but were <5 h after capture in all cases. None of these females had yet ovulated, and the ova in their largest developing modal groups averaged from 0.60 to 0.93 mm in diame-

TABLE 1.—Ovulatory status of skipjack tuna at different times following capture during June and July 1980.

Time	No.	Unovulated	Ovulating	Ripe	Spent
Refrigerated immediately after capture	16	16	0	0	0
Captive females, 0-5 h after capture[1]	9	9	0	0	0
Captive females, 5-6 h after capture	13	1	12	0	0
Captive females, 7-8.5 h after capture	12	3	1	8	0
Captive females, 15-65 h after capture	20	1	0	0	19

[1]Refrigerated after dying in transit to the laboratory; individual times of death not known, but <5 h after capture in all cases.

could be completed within 8 h after capture and occurred even in females that were so seriously traumatized that they died within a few hours after this time. Unless manually stripped, the ripe females released ova into the holding tank, and by the next day, 15 to 24 h after capture, were in a spent condition. Spawning behavior was not observed to occur. Instead, their behavior was invariably abnormal, as is typical for skipjack tuna during their first days in captivity, with individuals swimming aimlessly about the holding tanks.

The ovulated ova, both those released spontaneously into the tanks and those stripped from

TABLE 2.—Mean sizes (mm)[1] of ova in largest and second largest modal group of developing ova in skipjack tuna killed and refrigerated immediately after capture, or refrigerated after dying in transit to the laboratory.

	Refrigerated on capture			Died in transit			
Date	No.	Largest group	Second group	No.	Time (h)[2]	Largest group	Second group
15 July	4	0.62	Not measured				
		0.61	Not measured				
		0.59	Not measured				
		0.60	Not measured				
21 July	7	0.60	0.42				
		0.60	0.39				
		0.60	0.40				
		0.59	0.41				
		0.59	0.40				
		0.60	0.39				
		0.59	0.40				
22 July	3	0.22	0.10	7	<4.5	0.84	0.44
		0.64	0.41			0.93	0.43
		0.74	0.44			0.76	0.44
						0.69	0.44
						0.72	0.42
						0.70	0.42
						0.72	0.45
31 July	2	0.62	0.41	2	<5	0.67	0.41
		0.62	0.43			0.60	0.41

[1]Standard deviations 0.02-0.04
[2]Time between capture and death.

ter (Table 2). Of those kept alive, all but 1 of the 13 specimens examined 5 to 6 h after capture were ovulating but not yet ripe, while 8 of 12 examined after 7 to 8.5 h were ripe. Such ripe individuals yielded about 100,000 to over 150,000 ova when stripped. All but 1 of the 20 specimens examined 15 to 65 h after capture were spent. On all five occasions when the holding tanks were monitored for the presence of spawned ova, large numbers of ova were evident by the morning following delivery.

These observations clearly demonstrated that female skipjack tuna caught and kept alive during this time of year rapidly underwent the final stages of ovarian maturation and then ovulated ripe ova into the ovarian lumen. This response

ripe females, were normal in size and appearance. They were spherical, transparent, averaged about 1.0 mm in diameter, and had a single oil globule about 0.24 mm in diameter. The fertilization rate of ova stripped from females about 8 h following their capture was only about 40% to 50%; this may reflect the quality of the ova or the small amounts of viscous milt squeezed from the dissected testes. The embryos hatched in about 30 to 31 h at 25° to 26°C and started feeding on the third day after hatching. Although they fed actively on rotifers, *Brachionus* sp., and copepod nauplii, we were not able to rear any beyond the 12th day.

Numerous investigators have described the multimodal size distribution of developing ova in

the ovaries of maturing tunas. All of the ova in the most advanced modal group (about 0.60 mm or larger in these specimens) appeared to undergo final maturation and ovulation during this response but the second largest modal group seemed not to be affected. Ovaries from "control" specimens killed and refrigerated on capture and from those that died within 5 h contained an advanced modal group of maturing ova, as previously described, and a second, smaller modal group in which the ova averaged between 0.39 and 0.44 mm in diameter (Table 2). Ovaries from fully ovulated, ripe females and from recently spent females contained a residual modal group of similar, unovulated ova that averaged 0.39 to 0.49 mm in diameter (Table 3). These latter observations support the common assumption that in species with multimodal size distributions of developing ova, only the most advanced modal group will mature and be ovulated for a given spawning.

TABLE 3.—Mean sizes (mm)[1] of ova in largest modal group of unovulated ova in ripe or recently spent skipjack tuna.

Date	Hours after capture	Status	Ova diameter
28 June	8	Ripe	0.46
	8	Ripe	0.46
17 July	46	Spent	0.43
	46	Spent	0.40
21 July	7	Ripe	0.43
22 July	20.5	Spent	0.42
	25	Spent	0.39
23 July	[2]32-39	Spent	0.40
	32-39	Spent	0.43
	32-39	Spent	0.49
31 July	[2]6.5-15	Spent	0.45

[1]Standard deviations 0.02-0.04.
[2]Found dead in holding tanks, time interval since last seen alive.

Discussion

This rapid ovarian maturation, ovulation, and spawning appears to be a unique response to capture not previously reported. The trigger to this response is not known but appears related to stresses associated with capture and confinement. Witschi and Chang (1959) earlier concluded that ovulation of vertebrates could be facilitated by stress, but there has been a lack of direct evidence to support this conclusion. Indirect evidence for such a relationship within teleosts is suggested by ovulatory responses of certain species to treatment with corticosteroids (Hirose 1976; Sundararaj and Goswami 1977) and with epinephrine (Jalabert 1976), both of which have been reported to increase rapidly in serum concentrations following such stresses as handling and increased temperature (Mazeaud et al. 1977; Strange et al. 1977; Cook et al. 1980). The handling associated with being hooked, transported in crowded baitwells, transferred to shore tanks, and confined is obviously stressful and often fatal to newly captured skipjack tuna. Thermal stress may occur when they are confined in warm surface waters and prevented from returning to cooler depths after feeding.

Many additional aspects of this postcapture ovulatory response are not yet understood. Several aspects would be of particular interest: 1) the state of ovarian maturation that would be prerequisite for rapid egg development in females; 2) the seasonal availability of responsive females; 3) whether the time to complete ovulation, about 7 to 8 h in this study, will vary depending on such factors as water temperature, ovarian maturation, or time of day the fish are caught; and 4) whether this apparent response to acute stress is entirely an artificially produced anomaly, or whether it does have some relation to their natural spawning biology.

Past efforts to rear tunas in captivity (briefly reviewed by Kaya et al. 1981) had not heretofore resulted in dependable spawning procedures for any species. However, the occurrence and predictability of the ovulatory response to capture have now been applied to establish a routine procedure for spawning skipjack tuna at the Kewalo Research Facility. Additional spawnings have thus been accomplished during the summer of 1981, the second season of trials, and the response has been observed also in a second species of tuna—kawakawa, *Euthynnus affinis*. It would be of interest to determine whether other species will undergo a similar response to stresses of capture and confinement.

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ESTIMATING AND MONITORING INCIDENTAL DOLPHIN MORTALITY IN THE EASTERN TROPICAL PACIFIC TUNA PURSE SEINE FISHERY

Each year the purse seine fishery for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific is responsible for the incidental kill of thousands of small cetaceans,[1] primarily dolphins or "porpoise." Yellowfin tuna are often associated with small cetaceans in this region and fishermen have used this association since 1959 to catch tuna (McNeely 1961; Perrin 1969; Fox 1978). During the purse seining operation, cetaceans encircled with yellowfin tuna by the net may become entangled and accidentally drown. In such cases, the fishermen retain the tuna and discard the cetaceans at sea.

The Marine Mammal Protection Act of 1972 requires the tuna fishery to be managed so that the dolphin populations are maintained at specific population levels and that incidental mortality be reduced to insignificant levels. The National Marine Fisheries Service (NMFS) has the responsibility of monitoring the dolphin mortality and of assessing the impact of dolphin mortality on dolphin populations. NMFS carries out research on the abundance and distribution of dolphins, their biology, the level of incidental mortality, and methods for reducing incidental mortality.

Beginning in 1971, the NMFS regularly placed observers on purse seiners to collect data on the incidental mortality of dolphins. Prior to 1974, however, only a few observers were hired to collect data; the amount of data collected, therefore, is too small to produce a precise estimate of total incidental mortality. Most estimates from this period place the total at about 300,000 to 500,000 animals/yr. Estimates for 1974 and 1975, which are more precise, are 140,000 and 157,000 animals killed, respectively, for the U.S. fleet (Smith[2]).

After a U.S. District Court ruling in 1976, the NMFS set an annual quota of 78,000 animals for

[1]Dolphin, in this paper, is used as a general term referring to all small cetaceans impacted in the fishery. Mortality or kill refers to dolphin mortality incidental to the catch of yellowfin tuna. The unit of fishing effort "set" is defined as a single deployment of a purse seine net around an aggregation of dolphin or tuna. Tuna catches are expressed in the unit short tons, as it is the most common form in which these statistics are reported.

[2]Smith, T. D. Report of the status of porpoise stock workshop. Southwest Fish. Cent. Adm. Rep. LJ-79-41, 120 p.

1976 as the maximum allowable kill by the U.S. tuna fishery. Methods for monitoring the mortality levels, and projecting when the quota would be reached during the year, were required. A yellowfin tuna quota (175,000-195,000 short tons) managed by the Inter-American Tropical Tuna Commission (IATTC), around which the tuna fishermen planned their fishing operations, was also in effect and had to be incorporated into the procedure. In this paper, we describe statistical methods which have been used to estimate the annual incidental dolphin mortality for the U.S. fleet during the year and at the end of the year since 1976. This estimative procedure has been used also for foreign fleets by IATTC since 1979 (Allen and Goldsmith 1981).

Methods

The data sources used to monitor and estimate incidental dolphin mortality were the scientific observer program of the NMFS and the logbook records of the IATTC.

The NMFS observer program provides data on discarded dolphins. Trained technicians were placed aboard a random sample of U.S. tuna vessels to collect data of various types, including number of dolphins killed in a set, amount of tuna caught, species of tuna, fishing location, vessel capacity, and duration of trip.

The IATTC maintains a logbook system whereby it collects data on type of set, fishing locations, tonnage of catch, species of tuna, vessel carrying capacity, and other information that are recorded in logbooks by fishermen.

Three mortality rates were used to estimate total dolphin mortality. They were obtained by dividing the total observed kill of dolphins by the total observed number of dolphin sets (kill-per-set), by the total observed number of days-at-sea (kill-per-day), and by the observed total catch of yellowfin tuna associated with dolphin (kill-per-ton).

Estimation Procedures

Three estimation procedures were used in this study. The first procedure was based on kill-per-day statistics to monitor the dolphin mortality during the year; the second was based on kill-per-ton combined with kill-per-day to project the closure date; and the third was based on kill-per-set to estimate the total mortality at the end of the year.

The kill-per-day and the kill-per-set methods were based on stratified ratio estimators. Trips from which the dolphin set data were taken, were stratified according to fishing locality, vessel carrying capacity, yellowfin tuna catch, gear type, and fishing time. The fishing locality and time were directly related to the IATTC's yellowfin tuna regulatory system, which includes 1) an annual quota on yellowfin tuna catch within the Commission's yellowfin regulatory area (CYRA) (Fig. 1), 2) season closure to enforce the quota on yellowfin tuna catch, and 3) a "last trip" allocated at season closure to each vessel that fished during the open period (Table 1).

Kill-Per-Day Method

The kill-per-day method requires all trips to be stratified according to gear type, vessel carrying capacity, and fishing time; this method was developed to monitor kill during the season. The year was divided into three periods, each designating a trip type. Trip-type 1 included all vessel

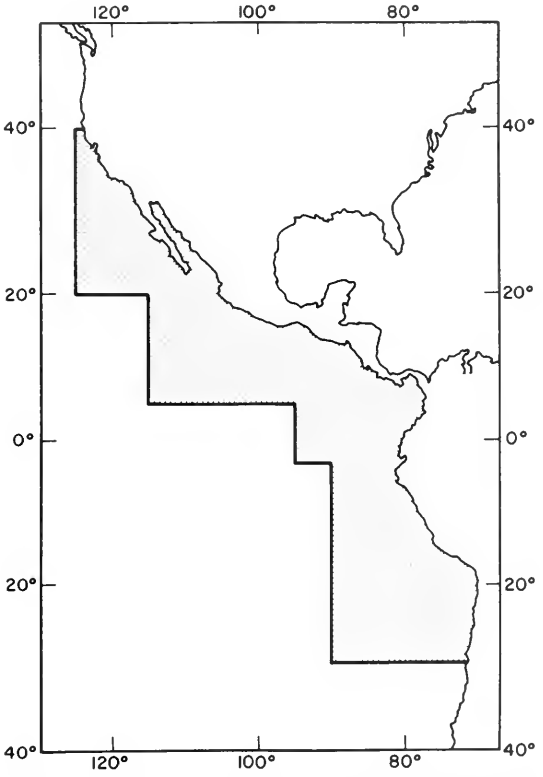

FIGURE 1.—The major part of the Inter-American Tropical Tuna Commission Yellowfin Regulatory Area (Courtesy of IATTC).

days through the IATTC season closure date (1 January through 26 March); trip-type 2 included all vessel days approximately corresponding to the "last trip" (27 March through 4 July); and trip-type 3 contained all vessel days after 4 July. This stratification of time was used to preclude overlapping trips. When a trip crossed a stratum boundary, it was assigned to more than one stratum. For example, for a trip lasting from 1 March to 5 May, the days from 1 March to 26 March would be assigned to trip-type 1, and days from 27 March to 5 May assigned to trip-type 2 (Table 1).

TABLE 1.—Layout of stratification of vessel trips (sets) for kill-per-day and kill-per-set methods.

Kill-per-day method with maximum 30 strata: 15 for each gear type						
NMFS vessel class	Trip 1 1 Jan.-26 Mar.	Trip 2 27 Mar.-4 July		Trip 3 5 July-end of fishing	
		open[1]	regulated	open[2]	regulated
I					
II					
III					

Kill-per-set method with maximum 32 strata				
IATTC vessel class	Successful sets		Unsuccessful sets	
	Inside CYRA	Outside CYRA	Inside CYRA	Outside CYRA
1				
2				
3				
4				
5				
6				
7				
8				

[1]Trips not subject to IATTC season closure. Most of them were "last trips."
[2]"Last trips" or trips made outside of CYRA.

The statistical formulation for dolphin mortality estimation according to a stratified ratio estimator is as follows (Cochran 1977):

For the ith stratum, $i = 1, \ldots, I$,
let N_i = total number of vessel trips
n_i = number of observed trips
X_{ij} = kill for the jth observed trip $j = 1, \ldots, n_i$
Y_{ij} = days-at-sea for the jth observed trip
r_i = kill-per-day
s_{r_i} = the approximate sample standard error of r_i (kill-per-day)
M_i = total number of days-at-sea
$\hat{T}_i$ = estimated total kill

then
$$r_i = \frac{\sum_j X_{ij}}{\sum_j Y_{ij}} \qquad (1)$$

$$s_{r_i}^2 = \frac{N_i - n_i}{N_i} \frac{r_i^2}{n_i} \left(\frac{s_x^2}{\bar{X}_i^2} + \frac{s_y^2}{\bar{Y}_i^2} - 2 \frac{\text{cov}(X,Y)}{\bar{X}_i \bar{Y}_i} \right)$$

where
$$s_x^2 = \frac{\sum_j (X_{ij} - \bar{X}_i)^2}{n_i - 1}$$

$$s_y^2 = \frac{\sum_j (Y_{ij} - \bar{Y}_i)^2}{n_i - 1}$$

and
$$\text{cov}(X,Y) = \frac{\sum_j (X_{ij} - \bar{X}_i)(Y_{ij} - \bar{Y}_i)}{n_i - 1}$$

$$\hat{T}_i = r_i M_i$$

$$\hat{T} = (\Sigma \hat{T}_i) = \Sigma r_i M_i$$

$$s_{\hat{T}}^2 = \Sigma M_i^2 s_{r_i}^2 .$$

The ratio estimator (r_i) and its approximate sample variance ($s_{r_i}^2$) are unbiased only under certain conditions (Cochran 1977). Alternative variance formulas have been suggested to correct the bias (Royall and Eberhardt 1975; Royall and Cumberland 1981). We chose the commonly used variance formula ($s_{r_i}^2$) in our procedure because the results of a simulation study showed that the bias of the ratio estimator and the approximate variance is negligible (Lo[3]). The simulation study was based upon the empirical dolphin mortality data collected in 1977.

Beginning on 30 June 1976, NMFS observers radioed their mortality counts to a shore base each month (starting in 1977, estimates were made biweekly). Data from this source were used to estimate cumulative mortality and to project the date when the annual quota would be reached.

Combined Kill-Per-Day and Kill-Per-Ton Method

The method using combined kill-per-day and kill-per-ton was developed to project at the end of

[3]Lo, N. C. H. Simulated results of a commonly used ratio estimator applied to incidental dolphin mortality by U.S. tuna purse seiners in the eastern tropical Pacific. Manusc. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

each month the date on which the quota would be reached. It included two procedural steps:

1. A series of cumulative dolphin mortality estimates for each future month was made by summing the current total mortality, based on kill-per-day statistics, and the projected mortality for future months, based on kill-per-ton statistics.

To calculate the projected cumulative mortality in future month m, we denote, at the end of month h,

$\hat{T}_h$ = the estimated current total mortality from the observed data by kill-per-day method

$\hat{T}_{m,h}$ = the projected cumulative mortality at the end of month m based upon T_h

U_m = the tonnage of yellowfin tuna catch in month m

$\hat{U}_m$ = the historical monthly tonnage average of yellowfin tuna catch

Z_W = observed kill-per-ton weighted by number of vessels of two gear types.

We then have

$$\hat{T}_{m,h} = \hat{T}_{m-1,h} + U_m \cdot Z_W \doteq \hat{T}_{m-1,h} + \hat{U}_m Z_W$$

$$= \hat{T}_h + \left(\sum_{i=h+1}^{m} \hat{U}_i\right) Z_W$$

for $m = h+1, h+2, \ldots, 12 \quad 1 \leq h \leq 11$

and $s^2_{\hat{T}_{m,h}} \doteq s^2_{\hat{T}_h} + \left(\sum_{i=h+1}^{m} \hat{U}_i\right)^2 s^2_{Z_W} + Z_W^2 \sum_{i=h+1}^{m} s_i^2$

where s_i^2 is the sample variance of yellowfin tuna catch for month i, and h refers to the month when the up-to-date total mortality was estimated, with the assumption that cov $(Z_W, \Sigma U_i)$ and cov (U_i, U_j) for $i \neq j$ are negligible. $s^2_{\hat{T}_{m,h}}$ is an approximate sample variance of $T_{m,h}$ by the Delta method (Seber 1973). $s^2_{Z_W}$ is the variance of weighted kill-per-ton. Z_W and $s^2_{Z_W}$ are based on the formulas of the ratio estimator (Equation (1)).

2. For quota Q, the projection of closure date was calculated as follows. If $Q < \hat{T}_{12,h}$, the month g was chosen where $\hat{T}_{g-1,h} < Q < \hat{T}_{g,h}$. The projected date (V) in month g was then obtained as:

$$V = \frac{Q - \hat{T}_{g-1,h}}{\hat{T}_{g,h} - \hat{T}_{g-1,h}} \cdot V_g$$

$$= \frac{Q - \left(\hat{T}_h + Z_W \sum_{i=h+1}^{g-1} \hat{U}_i\right)}{\hat{U}_g \cdot \hat{Z}_W} \cdot V_g$$

where V_g is the number of days in month g.

Kill-Per-Set Method

The kill-per-set method was developed to estimate the annual mortality at the end of the year. It requires that all dolphin sets be stratified in three ways: tonnage of yellowfin tuna catch during dolphin set, vessel carrying capacity, and fishing location (Table 1). Time of the year was not a separate factor as it correlated closely with fishing location.

The kill-per-set method was formulated in the same manner as the kill-per-day method (Equation (1)), except the auxiliary variable Y_{ij}'s were observed sets, r_i was kill-per-set, and M_i was total number of sets. In addition, the estimated total dolphin mortality was corrected for nonreporting in IATTC logbooks, inside and outside the CYRA, by a factor C, where C is the ratio of tonnage of yellowfin tuna taken with dolphin which were landed and weighed at port, to the tonnage of yellowfin tuna recorded in the logbooks as an estimate at sea. The mortality for strata without observed data was estimated with the kill-per-set of adjacent vessel-class strata. The resulting sample statistics are in Table 2.

TABLE 2.—Sample statistics[1] of kill-per-set method for 1976 U.S. purse seine tuna fleet.

IATTC vessel class	Inside CYRA			Outside CYRA		
	r_i	$S^2_{r_i}$	$X_i(n_i)$	r_i	$S^2_{r_i}$	$X_i(n_i)$
Successful sets:						
1	—	—	—	—	—	—
2	4.00	—	1(1)	—	—	—
3	—	—	—	—	—	—
4	3.02	2.17	68(5)	13.60	41.94	88(4)
5	7.08	4.42	37(4)	43.90	277.76	62(4)
6	10.60	15.51	44(4)	26.70	—	6(1)
7	17.60	7.72	148(1)	12.90	26.58	140(12)
8	22.00	19 62	32(2)	1.00	—	1(1)
Unsuccessful sets:						
1	—	—	—	—	—	—
2	0	—	1(1)	—	—	—
3	—	—	—	—	—	—
4	4.59	12.70	22(6)	9.90	22.95	10(3)
5	0.90	0.15	20(5)	4.50	8.24	8(2)
6	16.40	320.16	14(5)	8.31	27.91	—
7	3.15	0.28	20(4)	12.10	107.27	8(5)
8	3.27	7.78	22(2)	0	—	1(1)

[1] r_i = kill-per-set, $S^2_{r_i}$ = sample variance of r_i, X_i = number of observed dolphin sets, n_i = number of observed trips.

Results

The estimated mortality based on the kill-per-day method for each of the three periods was 24,000 animals (SE = 5,400) (1 January-26 March), 29,000 animals (SE = 5,300) (27 March-4 July), and 53,000 animals (SE = 21,000) (5 July-end of fishing), to give a total kill of 105,000 animals (SE = 22,000) for 1976 (Table 3).

Using the kill-per-set method, we computed dolphin mortality estimates adjusted for nonreporting of sets inside and outside the CYRA (Table 4). The estimated total dolphin mortality with this method was 104,000 animals (SE = 13,000).

The closure dates for reaching the quota of 78,000 animals as projected at the end of June, July, and September were in October. The fishery itself, however, was not actually closed until November, after a court hearing process.

The annual quotas for 1977, 1978, and 1979 were 52,000, 42,000, and 31,000 animals, respectively, and the mortality was monitored biweekly by species/stock. Due to the improvement and use of rescue techniques by the fishermen and the motivation of tuna fishermen to reduce dolphin mortality, the kill-per-day estimates of most of the species/stock have been below their annual quotas. The kill-per-set estimate for annual total dolphin mortality by U.S. seiners for 1977, 1978, and 1979 was 24,000 (SE = 3,500), 19,000 (SE = 3,700) and 18,000 animals (SE = 2,200), respectively.

Discussion

Procedures for estimating dolphin mortality have used the basic models tailored to suit the existing conditions of the fishery and available monitoring resources since 1976. The number of strata for the kill-per-day method has been reduced because only vessel classes II and III are fishing tuna with dolphin (the majority being class III vessels), and all the vessels are required to use a standard gear, i.e., super apron. Moreover, since 1979, there has been no quota on the yellowfin tuna catch. Thus, the entire year is "open" for fishing (Table 1).

The kill-per-set method is more precise than the kill-per-day method because the standard error is smaller. However, in order to make during-the-year estimates, procedures to collect accurate information on the number of dolphin sets for the whole fleet at regular intervals during the year, yet need to be developed. Analysis of use of the kill-per-set method indicated that the number of vessel classes (eight) was unnecessarily large. A revision of the stratification scheme for this method is currently in progress.

The statistical techniques of monitoring and estimating dolphin mortality can be applied to other kinds of incidental catches. The 1976 dolphin mortality data, in particular, demonstrated the complexity of the situation where the selection of auxiliary variables for ratio estimator and the stratification of data to reduce the variance were not straight forward. These factors have to be taken into account to ensure high precision of the estimates.

TABLE 3.—Estimated kill by U.S. vessels in 1976 using kill-per-day method.

	1 Jan.-26 Mar.		27 Mar.-4 July		5 July-end of fishing		1 Jan.-end of fishing	
Gear type	Kill	SE	Kill	SE	Kill	SE	Kill	SE
Conventional	23,769	5,448	24,884	5,316	47,068	20,531	95,721	21,896
Experimental	144	—	3,764	440	5,727	1,931	9,635	1,980
Total	23,913	5,448	28,648	5,334	52,795	20,622	105,356	21,985

TABLE 4.—Estimated kill by U.S. vessels in 1976 corrected for nonreported sets (SE in parentheses) using kill-per-set method.

Area	Tons YF on dolphin landed[1]	Tons YF on dolphin logged[1]	Correction factor C Column 2 ÷ column 3	Adjusted kill
CYRA	55,112	47,180	1.17	44,061 (4,424)
Outside	70,745	65,248	1.08	55,801 (12,690)
Total				99,862 (13,439)
Experimental and chartered vessels				4,211 (—)
Grand total				104,073 (13,439)

[1]IATTC record.

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WHITE DALL'S PORPOISE SIGHTED IN THE NORTH PACIFIC

Several studies on the population and distribution of marine mammals were conducted between 1978 and 1981 in the North Pacific Ocean under a United States-Japan cooperative agreement of the International Convention for the High Seas Fisheries of the North Pacific Ocean. During that period, two white Dall's porpoise, *Phocoenoides dalli*, were sighted.

Two of the authors (Joyce and Ogasawara) sighted one such color variant (Fig. 1) at 1410 h (JST) on 29 July 1980, 8 km south of Kushiro, Japan (lat. 42°52. 5′N, long. 144°21.5′E), while aboard the RV *Hokushin Maru*. The water depth was 70 m and the sea surface temperature was 17.5°C. The animal was estimated to be 190 to 210 cm long and was accompanied by a normally colored Dall's porpoise, dalli type, of the same size. Both animals approached the vessel and rode the bow wave for 5 min. The white animal surfaced once every 5 to 6 s and created a "roostertail" splash, typical of the Dall's porpoise. It was completely white except for a slight gray shading along the dorsal ridge between the dorsal fin and the flukes, and along the posterior edge of the blowhole. There was no color differentiation where the black-white border usually occurs on the lateral surface. Other than color, there were no physical or behavioral characteristics to distinguish this animal from other Dall's porpoise.

Another white Dall's porpoise was sighted by Rosapepe on 13 August 1980, 25 km west of the Washington State coast (lat. 45°26.5′N, long. 124°15.6′W), while aboard the NOAA vessel *Miller Freeman*. The animal was all white except for a brownish area on the dorsal surface, between the blowhole and the dorsal fin. It was seen with three Dall's porpoises, dalli type, of normal coloration. All four animals approached the vessel and rode the bow wave for 7 min.

The Dall's porpoise is known to exhibit two and possibly three color variations (Morejohn 1979). The dalli type, the original type described, is mostly black, with a white area on the ventral and lower lateral surfaces, originating in line with the anterior insertion of the dorsal fin and extending posterior of the genital slit (True 1885). The truei type is differentiated by the anterior extension of the white area to the anterior insertion of the pectoral flipper (Andrews 1911). The truei type was once classified as a separate species by Andrews (1911) but was later described as a color variant (Cowan 1944). The taxonomic status of this type is still in question. All black Dall's porpoise have been described (Wilke et al. 1953; Nishiwaki 1966), as has the gray or striped variant (Wilke et al. 1953; Morejohn et al. 1973). However, the white variant has not previously been described, indicating that this colormorph, possibly caused by albinism, occurs rarely.

Acknowledgments

Marine mammal research aboard the *Miller Freeman* was sponsored by the Platforms of Opportunity Program, National Marine Mammal Laboratory (NMML), NMFS. U.S. marine mammal studies aboard the *Hokushin Maru*

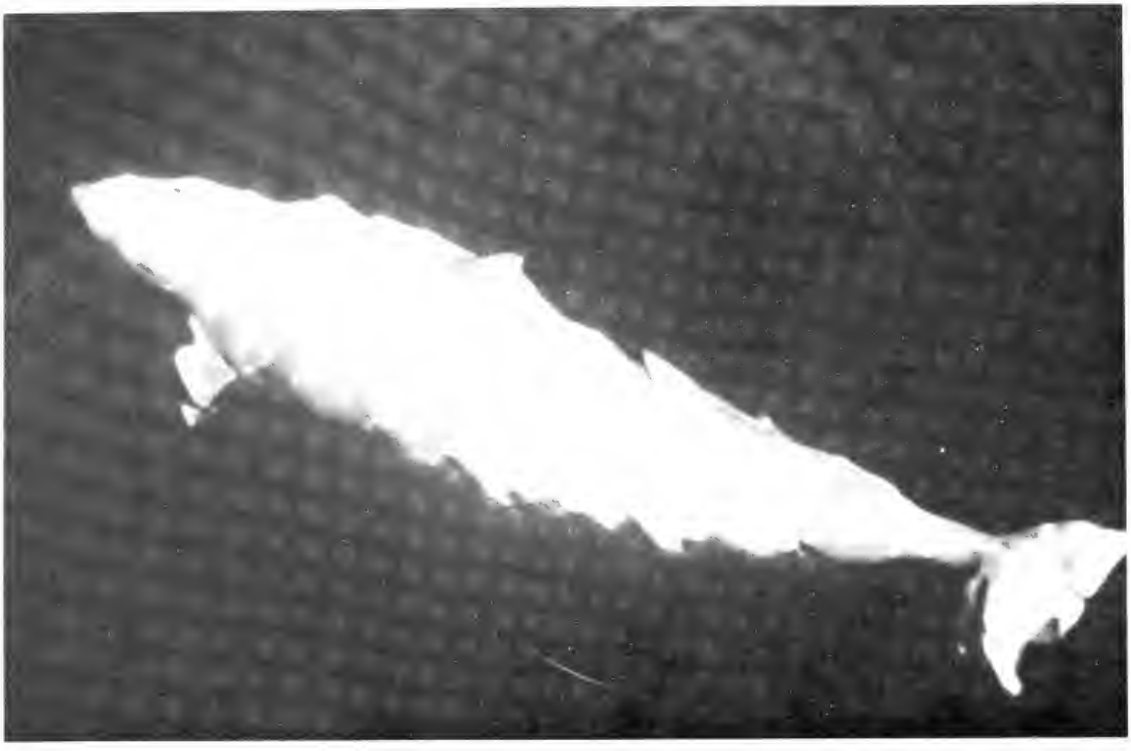

FIGURE 1.—A color variant of a white Dall's porpoise, *Phocoenoides dalli*, sighted 8 km south of Kushiro, Japan, from the Japanese research vessel *Hokushin Maru*.

were supported by the Dall's Porpoise Project, NMML, NMFS, and were made possible by the cooperation of the Japanese Fisheries Agency, through an agreement of the International Convention for the High Seas Fisheries of the North Pacific Ocean. H. Braham, M. Dahlheim, and L. Jones reviewed this paper.

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NOTICES

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747. Movement, growth, and mortality of American lobsters, *Homarus americanus*, tagged along the coast of Maine. By Jay S. Krouse. September 1981, iii + 12 p., 10 figs., 8 tables.
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Notes

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Fishery Bulletin

Vol. 80, No. 3 July 1982

(Continued on back cover)

Seattle, Washington

Fishery Bulletin

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

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Seattle, Washington

1982

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Notes

DEVELOPMENT OF EGGS AND LARVAE OF THE WHITE CROAKER, *GENYONEMUS LINEATUS* AYRES (PISCES: SCIAENIDAE), OFF THE SOUTHERN CALIFORNIA COAST

WILLIAM WATSON[1]

ABSTRACT

Eggs and larvae of the white croaker, *Genyonemus lineatus*, were collected near the San Onofre Nuclear Generating Station in 1978 and 1979. A developmental series based on 59 eggs and 168 larvae and early juveniles was assembled.

Live *G. lineatus* eggs are pelagic, transparent, and spherical, averaging 0.85 mm in diameter with a single oil droplet of 0.23 mm. Preserved, newly hatched larvae average 1.57 mm SL and are not well developed. Larval development is a gradual process. Notochord flexion begins at ca. 5.4 mm SL and is complete by ca. 6.4 mm SL. Dorsal and anal fin anlagen appear at ca. 5 mm SL and the full complement of rays is present in each fin by ca. 8.2 mm SL. Pelvic differentiation begins at ca. 5.3 mm SL and is finished by ca. 8.6 mm SL. Pectoral rays begin to develop at ca. 7.8 mm SL and all are present by ca. 13 mm SL.

Larval pigmentation is largely restricted to the dorsum at hatching, but migrates to the ventral midline during early development. Melanophores are restricted to the ventrum and gut through much of the subsequent larval period. A barred pattern develops during transition to the juvenile stage.

Genyonemus lineatus larvae are distinguishable from similar cooccurring species by the presence of a nape melanophore and larger melanophores in the midventral trunk series at myomeres 9-10 and 16-18.

The sciaenid genus, *Genyonemus*, is represented by a single species, *G. lineatus* (Ayres), the white croaker. It occurs along the west coast of North America from central Baja California to southern British Columbia (Miller and Lea 1972), although its numbers are reduced north of San Francisco, Calif. (Frey 1971). In southern California the white croaker is a common inshore species of modest sport and commercial value (Skogsberg 1939; Frey 1971). Its larvae rank second in abundance only to those of the northern anchovy, *Engraulis mordax*, among the inshore ichthyoplankters off San Onofre, Calif. (Walker et al. 1980[2]).

Despite its abundance in southern California, the early life history of *G. lineatus* is poorly known. Seasonal spawning cycles are described based on gonadal studies (Goldberg 1976), and the duration of the egg stage is mentioned by Morris (1956), who reared *G. lineatus* from field-collected eggs through 19-d-old larvae. Larvae are not described, although Morris (1956) gives dimensions of the egg.

Beginning in January 1978, Marine Ecological Consultants of Southern California initiated a study of the inshore ichthyoplankton off San Onofre (Fig. 1) for the Marine Review Committee of the California Coastal Commission (Barnett and Sertic 1979[3]). During this study approximately 48,000 *G. lineatus* larvae were sorted from the samples, providing an opportunity to construct a developmental series through the early juvenile stage. Live plankton samples provided eggs for rearing purposes. This paper describes the egg and larval development of *G. lineatus* as determined from these series.

MATERIALS AND METHODS

Egg and larval descriptions are based on detailed observation of 59 eggs, 29 reared larvae,

[1]Marine Ecological Consultants, 533 Stevens Avenue, Solana Beach, CA 92075.

[2]Walker, H. J., A. M. Barnett, and P. D. Sertic. 1980. Seasonal patterns and abundance of larval fishes in the nearshore Southern California Bight off San Onofre, California. Marine Ecological Consultants of Southern California, 533 Stevens Ave., Solana Beach, CA 92075, 16 p.

[3]Barnett, A. M., and P. D. Sertic. 1979. Preliminary report of patterns of abundance of ichthyoplankton off San Onofre and their relationship to the cooling operations of SONGS. Marine Review Committee Document 79-01, p. 1-1 to 4-5. Marine Review Committee of the California Coastal Commission, San Francisco, Calif.

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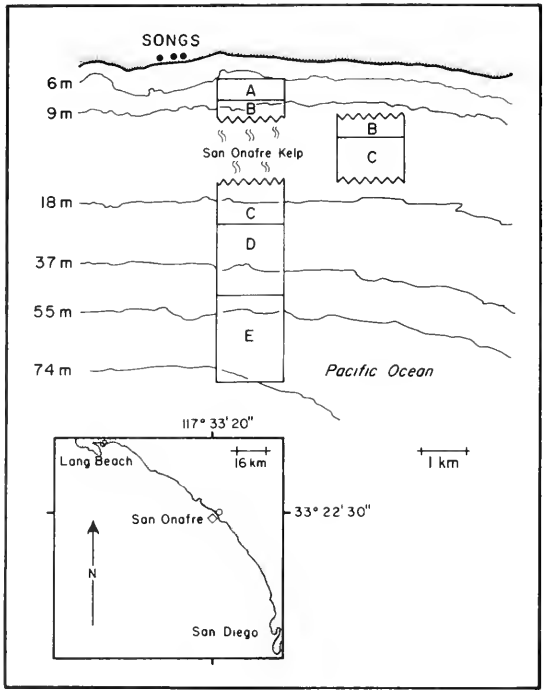

FIGURE 1.—Chart of the sampling area and its position off the southern California coast. SONGS = San Onofre Nuclear Generating Station.

and 139 field larvae. These were collected in 1978 and 1979 between the 6 and 20 m isobaths near the San Onofre Nuclear Generating Station (Fig. 1; Barnett and Sertic footnote 3).

Eggs used only for egg description were maintained at ambient air temperature (ca. 20°C) while those reared for larval description were maintained near their collection temperatures (13.4°-14.3°C). The sequence of developmental events in reared specimens was confirmed by comparison with field specimens.

Plankton samples were preserved in the field in 5% seawater-Formalin[4] and specimens later sorted in the laboratory. These were stored in 2.5-5% seawater-Formalin. Reared specimens were preserved in 2.5% seawater-Formalin.

Because reared *Genyonemus* larvae often are more heavily pigmented than field specimens, the latter were used as the principal descriptive source. Yolk-sac larvae were primarily reared specimens, owing to the difficulty of obtaining undamaged field specimens of this size. Twenty field specimens from the early larval stage through transition to the juvenile were cleared and stained with alizarin following the method of Hollister (1934) to determine the sequence of skeletal ossification.

Measurements were made to the nearest 0.03 mm at 25× using a binocular dissecting microscope equipped with an ocular micrometer. Drawings were made with the aid of a camera lucida. Pigmentation illustrated for yolk-sac larvae represents fresh material; the pattern is largely lost after several weeks of preservation.

Developmental stages follow the terminology of Ahlstrom and Ball (1954), except that the transitional period between the larval and juvenile stages is considered to begin when the first scales appear and to end when scalation is essentially complete. All fin rays and myomeres (preanal plus postanal) were counted on each specimen, when distinguishable. Dimensions measured were body depth, eye diameter, head length, preanal length, preanal fin length, snout length, and standard length. These dimensions are defined in the literature (e.g., Saksena and Richards 1975; Powles 1980).

EMBRYONIC DEVELOPMENT

The *G. lineatus* egg is pelagic, spherical or nearly so, and transparent, with an unsculptured chorion and unsegmented yolk (Fig. 2). It usually contains a single colorless to slightly yellowish oil droplet, although in the early stage it may contain two or three oil droplets which later coalesce. Thirty-eight live eggs collected from the plankton averaged 0.85 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.23 mm (SD = 0.02 mm). The perivitelline space was very small (<0.04 mm). These dimensions are similar to those given by Morris (1956) for *G. lineatus* eggs collected from the plankton: egg diameter 0.9 mm and oil droplet diameter 0.2 mm. Twenty-one eggs preserved for 111 d in 2.5% seawater-Formalin were slightly oval, averaging 0.84 by 0.83 mm (SD = 0.02 mm) in diameter, with a single oil droplet of 0.21 mm (SD = 0.01 mm) and a perivitelline space of 0.05 mm (SD = 0.02 mm).

The embryo is unpigmented through gastrulation (Fig. 2a, b). During eye capsule formation the first few small melanophores appear on the distal side of the oil droplet and on the yolk adjacent to the oil droplet (Fig. 2c). Midlateral, middorsal, and a few scattered dorsolateral trunk

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

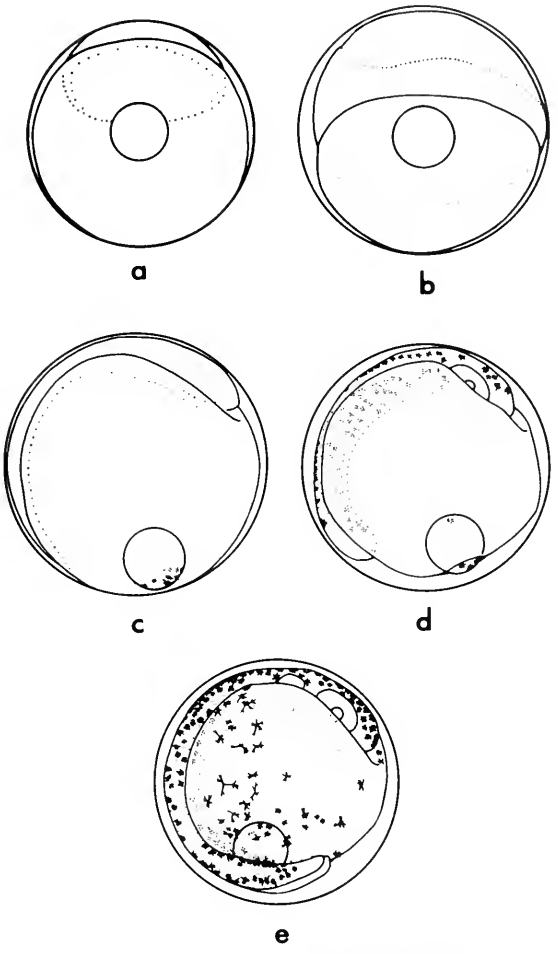

FIGURE 2.—Development of the *Genyonemus lineatus* egg: a) blastula stage, 0.78 mm diameter; b) gastrula stage, 0.86 mm diameter; c) early embryo just prior to blastopore closure, 0.90 mm diameter; d) tail bud stage, 0.84 mm diameter; e) late stage, 0.84 mm diameter. All illustrations are of live eggs. Note that oil droplets are somewhat smaller than average in this group of eggs.

melanophores appear shortly thereafter. About 5 h after eye capsule formation (at 20°C) small melanophores surround the trunk and are scattered dorsally on the head (Fig. 2d). A few melanophores occur on the yolk adjacent to the tail bud at this stage. As development continues the dorsal head pigmentation increases and trunk melanophores become situated primarily dorsally and dorsolaterally. Yolk melanophores increase in number until they nearly surround the yolk just before hatching (Fig. 2e).

The oil droplet is located opposite or adjacent to the embryo through gastrulation (Fig. 2a, b). During the latter part of the egg stage the tail of the developing embryo grows past the oil droplet, which ultimately is situated adjacent to the embryo just anterior to the anus (Fig. 2e).

Optic capsules develop almost simultaneously with blastopore closure and just prior to somite development. Lens development begins at about the four myotome stage.

Somite differentiation begins just behind the head and continues posteriorly. Kuppfer's vesicle first becomes apparent near the tip of the tail bud at about the 4 somite stage and persists to the 18 somite stage. Heart and finfold development are initiated at about the 18 somite stage and the tail first separates from the yolk shortly thereafter. By the end of the egg stage the embryo has 25-26 myomeres, otic capsules with at least the sagittae developing, a simple tubular gut, wide finfold, and functional heart.

Preserved eggs collected from the plankton at 1900 PST on 29 January 1979 were largely in the two, four, and eight cell stages. Live eggs from the same sample began gastrulation after 20-22 h of incubation (ca. 20°C) and eye capsules developed at about 26-28 h. The 18 somite stage was reached at about 38-40 h and the full somite complement attained by 43-45 h. All larvae had hatched by 52 h.

YOLK-SAC LARVAE

Pigmentation

The pigmentation of newly hatched larvae closely resembles that of late stage eggs, with melanophores concentrated primarily dorsally and dorsolaterally on the head and trunk (Fig. 3a). Additional pigment includes a characteristic large dendritic melanophore extending upward from the nape to the margin of the finfold, a large midventral melanophore about halfway between the anus and tip of the tail (one or two small lateral melanophores may occur here as well), and one to three small middorsal and midventral melanophores near the tip of the notochord. One or two melanophores usually occur ventrally on the gut, near the anus. Oil droplet pigmentation is mainly proximal. A few melanophores are usually scattered on the yolk sac. The nape, oil droplet and gut, and midtail pigment appears as three distinct bands in live larvae. Only the nape and midtail melanophores may be expected to survive prolonged Formalin preservation.

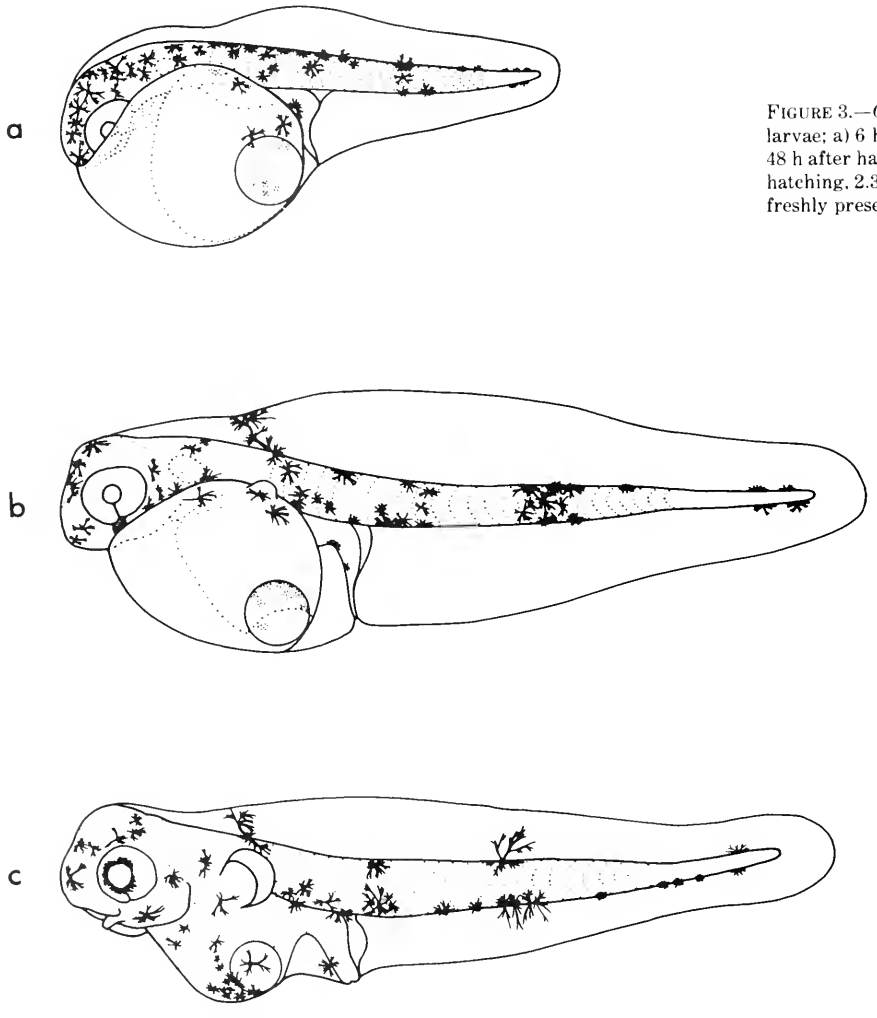

FIGURE 3.—*Genyonemus lineatus* yolk-sac larvae: a) 6 h after hatching, 1.54 mm; b) 48 h after hatching, 2.48 mm; c) 68 h after hatching, 2.36 mm. All illustrations are of freshly preserved reared larvae.

Head pigment changes little during the first 60 h (ca. 13°C). After this it condenses to a few melanophores over the forebrain and midbrain. These melanophores may be lost by the end of the yolk-sac stage except for one or two melanophores on the otic capsule. A small melanophore first appears at the angular bone just at the end of the yolk-sac stage. Eye pigmentation begins at about 60 h (Fig. 3c) and is complete by 120 h after hatching (ca. 13°C).

During the first 24 h after hatching the dorsal trunk melanophores begin to migrate ventrally, condensing into bands at the nape, the anus, and midtail at myomeres 16-18 (Fig. 3b). This pattern persists but becomes indistinct as melanophores continue to migrate ventrally.

By the end of the yolk-sac stage dorsal trunk pigment consists only of the large nape-finfold melanophore, one or two smaller melanophores near the level of the anus, one in the region of myomeres 16-18, and one or two near the tip of the notochord. Lateral melanophores may persist in these same areas, although more often they do not. Midventral trunk pigment increases to a series of 8-10 melanophores, with those at myomeres 9-10 and 16-18 usually larger.

Oil droplet and yolk-sac pigment changes only by condensing as the yolk is consumed. The ventral hindgut melanophores persist through the yolk-sac stage with the lower migrating to a position adjacent to the anus. A single small melanophore usually moves to the dorsal midline of the hindgut where the hindgut turns downward at the fifth or sixth myomere. After about 60 h one

or two melanophores may overlie the gut at the level of the soon-to-inflate swim bladder at myomeres 1 and 2.

Morphology

Genyonemus lineatus larvae hatch in a relatively undifferentiated state with unpigmented eyes, otic capsules usually with sagittae, a functional but simple tubular heart, straight tubular gut, large yolk sac, and posterior oil droplet. No mouth, branchial apparatus, or other viscera are apparent.

Pectoral buds appear during the second day after hatching and pectoral membranes are present on the third. The mouth opens and the operculum becomes discernible during the third day. Gut differentiation begins at this time. Yolk exhaustion and swim bladder inflation occur on the sixth day. Feeding, and consequently the end of the yolk-sac stage, is initiated during the sixth or seventh day after hatching (at ca. 13°-14°C).

Larvae lengthen during the yolk-sac stage, from a preserved hatching length of 1.57 mm ($n = 4$, SD = 0.02 mm) to 2.41 mm ($n = 4$, SD = 0.02 mm) at yolk exhaustion. Yolk-sac length declines from 0.86 mm ($n = 4$, SD = 0.04 mm) at hatching to zero. Head length, preanal length, and eye diameter change little during the yolk-sac stage.

LARVAE

Pigmentation

Genyonemus lineatus larvae are quite variable in degree of pigmentation (e.g., midwinter larvae often are more lightly pigmented than spring larvae), although the basic pattern is conservative. Because of this variability, pigmentation is described more fully than might otherwise be warranted. Illustrations are of typical (i.e., late winter) specimens.

The head typically is moderately pigmented at the beginning of the larval stage (Fig. 4a). Single small melanophores are nearly always present on the snout and at the angular bone, as many as four or five may be scattered over the fore- and midbrain regions, and one or two are often located in the floor of the otic capsule. Some specimens have an elongate melanophore laterally on the mandible.

The snout melanophore is lost soon after yolk absorption and the snout remains unpigmented throughout larval development. Small melanophores begin to appear between the nostrils at ca. 17 mm and rapidly proliferate to form a band which persists until becoming obscured by the increasing head pigmentation in the juvenile stage.

The melanophore at the angular bone persists through the juvenile stage. Mandibular pigment typically is absent until the beginning of transition at ca. 13 mm, when a pair of melanophores appears at the center of the mandible. The number increases to six or eight by the beginning of the juvenile stage (ca. 17 mm). Premaxillary pigmentation begins shortly before transition, with a pair of melanophores at the center of the upper jaw. Four to six more melanophores are added by the beginning of the juvenile stage. Some small specimens may have one or two melanophores in the central gular region. These rarely persist beyond ca. 5 mm.

Pigment on top of the head declines rapidly early in the larval stage, and is absent after ca. 2.8 mm. During the transitional period melanophores again appear on the head, beginning with a pair over the midbrain region at ca. 14.8 mm. Melanophores rapidly proliferate to form bands over the midbrain by the beginning of the juvenile stage.

Opercular pigmentation is acquired just before the juvenile stage, with a pair of melanophores under the central opercular region. One or two external melanophores develop on the upper operculum at ca. 17.2 mm and quickly increase in number to form a dark patch.

Otic floor pigment is most often present in larvae <4 mm and absent in larger specimens. At ca. 9.5 mm a melanophore appears under the anterior hindbrain, followed by an anterolateral melanophore on each side at ca. 10 mm. A second ventrolateral melanophore is acquired here during transition (ca. 13 mm) and by the beginning of the juvenile stage the anterior hindbrain is usually surrounded by a heavy pigment band.

At the beginning of the larval stage dorsal trunk pigment includes one or two nape-finfold melanophores, usually a single middorsal melanophore between myomeres 16 and 18, often a middorsal or dorsolateral melanophore between myomeres 6 and 8, and occasionally one or two small middorsal melanophores near the tip of the notochord (Fig. 4a). Lateral trunk pigment which persists into the larval stage is located at myomeres 6-8 and 16-18. This usually is lost by 2.8 mm although an occasional specimen of any

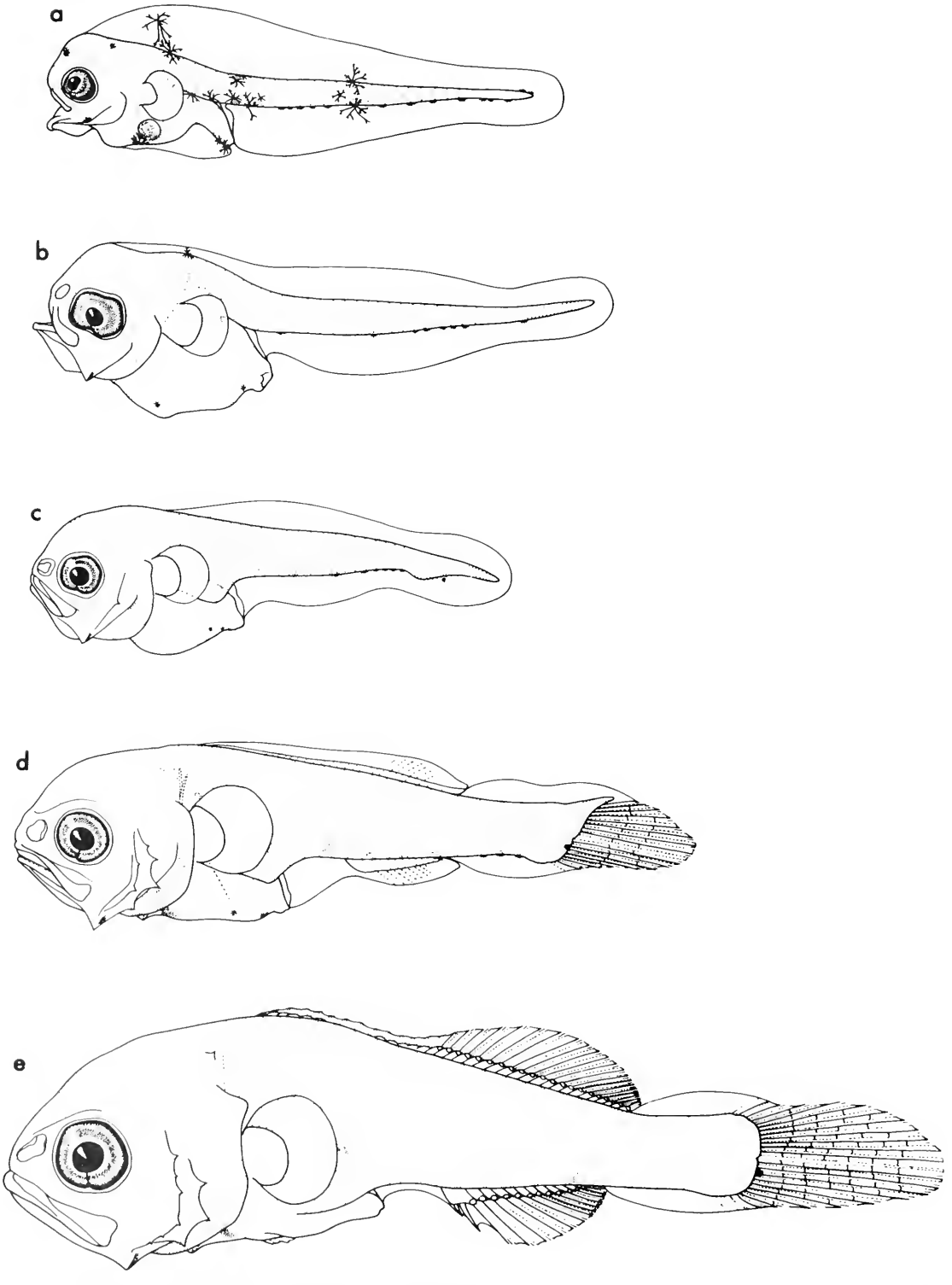

FIGURE 4.—*Genyonemus lineatus* larvae: a) 2.73 mm; b) 3.04 mm; c) 5.15 mm; d) 6.18 mm; e) 8.16 mm. All illustrations are of field specimens.

size may retain a midlateral melanophore in the myomere 16-18 region. The ventral midline melanophore series increases quickly from 8 to 10 late in the yolk-sac stage to 15-21 by ca. 2.6 mm. The melanophores at myomeres 9-10 and 16-18 remain largest.

The dorsal notochord tip melanophores and those at myomeres 6-8 are lost by ca. 2.8 mm (Fig. 4b). The melanophore at myomeres 16-18 often persists to 5 mm, and may continue until 6 mm in some specimens. The nape melanophore migrates internally and is obscured by the overlying tissue as early as ca. 2.5 mm or as late as ca. 6.1 mm, but most often between 4.8 and 5.6 mm. Following the internal migration of the nape melanophore the trunk remains unpigmented dorsally and laterally through the larval and transitional periods. Early in the juvenile stage a barred pattern develops (Fig. 5). At 17.2 mm a short bar crosses the nape and may extend laterally to the level of the supracleithral spine. A second bar extends to the midlateral line from dorsal spines VII-X, a third and fourth from dorsal rays 5-10 and 16-21, and a fifth crosses the peduncle. Six to nine bars ultimately develop in the juvenile stage, counting the snout and cranial bars. Trunk melanophores in these bars are principally myoseptal.

The midventral trunk melanophores number between 15 and 21 at the beginning of the larval stage. They begin coalescing immediately, but from 7 to 19 remain through 4.5 mm. By the beginning of caudal flexion (ca. 5.5 mm) they decline to between 2 and 12, and thereafter number between 2 and 6. The melanophore between myomeres 16 and 18 is always largest and persists through the larval stage (Fig. 4e). This melanophore lies at the posterior end of the anal fin in older larvae. The second largest midventral melanophore, which initially lies between myomeres 9 and 10, shifts one to three myomeres posteriorly and migrates internally by the time of anal fin anlage formation (Fig. 4c, d). It often persists through the larval stage, lying near the anal fin origin in older specimens. One to three small melanophores may also remain in the ventral midline between myomeres 20 and 25 through the larval period. One small melanophore usually persists near the end of the notochord, becoming located at the central distal margin of the developing hypural complex during flexion. As the caudal fin rays ossify, one to a few melanophores develop along the central and lower fin ray bases. During transition internal melanophores begin to appear along the urostyle and lower hypurals, and a band of pigment develops along the distal one-third of the caudal rays.

Soon after anal fin completion melanophores develop at the anal fin ray bases. These occur first on either side between anal soft rays 1 and 4, and proceed both anteriorly and posteriorly. The number of melanophores is variable—usually three or fewer in larvae <9 mm and five or fewer in larger specimens.

The gut region is moderately pigmented at the beginning of the larval period: a single external melanophore normally lies on each side just behind the upper pectoral insertion; one to three pairs of melanophores occur on top of the swim

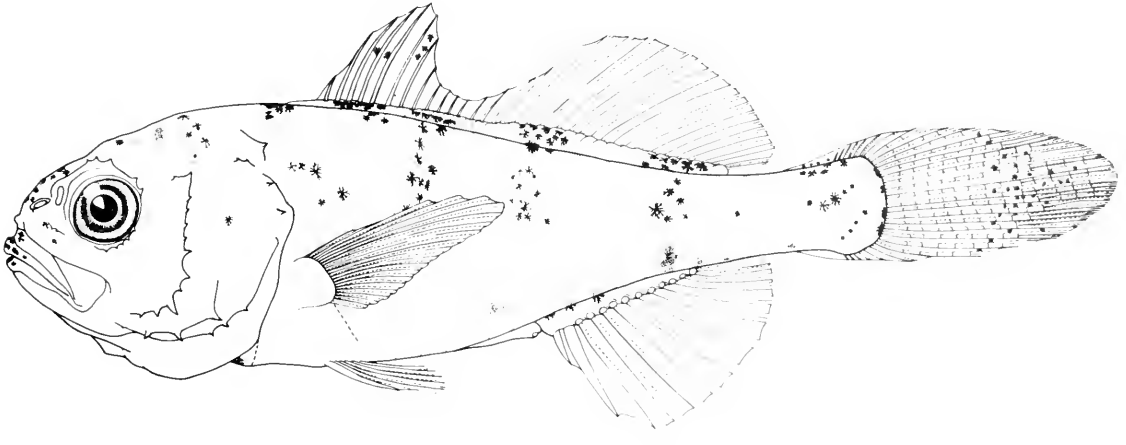

FIGURE 5.—*Genyonemus lineatus* early juvenile, 19.20 mm.

bladder; as many as two lie on the middorsal surface on the gut just behind the swim bladder; one small melanophore usually lies on the dorsal hindgut just where it turns downward at myomere 5 or 6; a larger melanophore lies adjacent to the hindgut just anterior to the anus, one rather large melanophore may lie on the anterior midline of the visceral mass just below the level of mideye; none to several small melanophores are scattered ventrally and ventrolaterally over the anterior gut.

Gut pigment generally decreases during larval development. The melanophore behind the pectoral base rarely persists beyond 5.2 mm. Swim bladder pigment increases but remains restricted to its dorsal surface through the larval period. All other dorsal gut pigment except the melanophore on the hindgut is lost by ca. 3 mm and usually does not reappear until ca. 11.2 mm, near the end of the larval stage. The dorsal melanophore on the hindgut is present more often than not (present in 63% of the larvae examined) and is nearly always quite small in specimens smaller than ca. 8 mm. In larger specimens it is nearly always present (in 95% of the larvae examined) and increases in size (occasionally others are added as well) to nearly cover the dorsal surface on the hindgut by ca. 11.2 mm (Fig. 5). In older specimens melanophores begin to fill in between the swim bladder and hindgut, so that in early juveniles the dorsal gut cavity is often entirely pigmented.

The melanophore just anterior to the anus usually persists through ca. 6 mm but is rarely present in larger specimens. Other ventral gut pigment is quite variable early in the larval period, ranging from one to several melanophores typically on the anterior half of the gut. The ventral midline of the gut often remains unpigmented throughout larval life. Only a single melanophore just anterior to the cleithral symphysis commonly remains after 5 mm (present in 64% of the larvae examined). During the transitional period one or two additional melanophores develop to form a series along the midline of the isthmus. After completion of the pelvic fin (ca. 9 mm) a single melanophore may appear between the pelvic bases. During transition a ventral midline series of two or three melanophores may arise behind the pelvic fin bases.

The large internal melanophore located anteriorly on the upper visceral mass migrates ventrally as larval development proceeds: when present it is nearly always on the upper visceral mass in larvae smaller than ca. 4 mm, is most frequently located halfway down between 4 and 6 mm (Fig. 4c), and is nearly always present at the lower anterior margin of the visceral mass in specimens larger than ca. 6 mm (Fig. 4d).

Fin Development

At the beginning of the larval period *G. lineatus* larvae have only a broad medial finfold and pectoral fin without rays. Subsequent fin development follows a typical sciaenid sequence (e.g., Powles 1980; Pearson 1929).

The caudal fin is first to develop. The caudal anlage appears at ca. 3.8 mm and the central four to six principal rays begin to ossify at ca. 4.8 mm. Notochord flexion begins at ca. 5.4 mm and is complete at ca. 6.4 mm. The full complement of 9+8 principal caudal rays is ossified by the end of flexion. Further development includes the addition of secondary caudal rays (15 to 17 total by the early juvenile stage), branching of the central principal rays and lengthening of the fin. The central rays are longest throughout larval development.

Anal and dorsal fin anlagen appear nearly simultaneously at ca. 5 mm. The anal fin anlage is short, usually extending between myomeres 13 and 18. Differentiation begins with the most anterior anal soft ray bases just after the anlage first appears, and proceeds posteriorly. The sequence of anal fin ray differentiation follows that of the ray bases, beginning with the first soft ray at ca. 6 mm and proceeding posteriorly. All anal soft rays are discernible by ca. 6.7 mm, at which time the second anal spine begins to ossify. The first anal spine completes the anal fin ray complement at ca. 7.2 mm. Subsequent larval development consists of lengthening of the rays and ossification of the pterygiophores.

The dorsal anlage initially lies between the tenth and fifteenth myomeres and lengthens to myomeres 3-21 by ca. 6 mm. As in anal fin development, the anterior soft ray bases differentiate first, beginning at ca. 5.4 mm, and the soft rays ossify from the first ray posteriorly beginning at ca. 6 mm. The posterior 8 to 10 bases are undifferentiated as the first soft rays begin ossifying. Dorsal spine bases begin differentiating anteriorly at ca. 6.4 mm and the anterior spines appear at ca. 7.2 mm, about the time of acquisition of the full complement of dorsal soft rays. The dorsal spines ossify posteriorly, reaching the adult complement of 12 to 15 by 8.0-8.5 mm. The

dorsal fin is continuous, with the first dorsal much lower than the second initially. As growth continues the anterior spines (except the first) lengthen faster than the others, so that the dorsal fin is deeply notched by the beginning of the transitional period.

Pelvic fin buds first appear between 5.3 and 5.9 mm and the first one or two elements become visible at ca. 7.2 mm. Differentiation of rays proceeds toward the midline. The full complement of one small spine and five rays usually is attained by ca. 8.6 mm.

Pectoral rays first develop at ca. 7.8 mm, beginning from the upper pectoral base and proceeding downward. Five to nine upper rays are present by ca. 8.6 mm and the full complement of one small spine plus 17 to 18 rays is attained by ca. 12.7 mm, just before the transition to the juvenile stage. The upper pectoral rays lengthen much more than the lower rays as the fin grows, changing its outline from rounded to bluntly pointed.

Head Spination

Genyonemus lineatus acquires a number of small spines on the head during larval development. First among these is the spine at the angle of the preopercle at ca. 3.5 mm. A second spine is added just above the angle and a second row of preopercular spines begins developing at ca. 4.5 mm. Preopercular spination subsequently increases to between five and eight short spines in each row by the end of the larval period. Early juveniles may have as many as 12 spines in each row. An interopercular spine develops at ca. 5.5 mm. Interopercular spines vary in number between one and four throughout larval development. A subopercular spine develops at ca. 10.5 mm; as many as two or three may be present at the beginning of the juvenile stage. An opercular spine first appears at ca. 10.5 mm and remains throughout subsequent development.

A minute supracleithral spine emerges at ca. 6.6 mm. Up to three additional supracleithral spines may develop during the transition to juvenile.

The first supraocular spine becomes apparent at ca. 7.2 mm and is joined by an additional one or two spines by ca. 9.2 mm. As many as eight small supraocular spines may be present by the end of the transitional period.

Ossification

Initial skeletal ossification in *G. lineatus* begins with the cleithra. This is soon followed by the jaws and associated bones, some of the branchiostegals, opercular apparatus, and branchial apparatus, and the posterior skull. Premaxillary teeth appear next, followed by the first pharyngeal teeth. Dentary teeth arise later, about the beginning of vertebral and principal caudal fin ray ossification. Initiation of dorsal and anal soft fin ray and hypural ossification follows (Table 1). Anal fin spines precede the dorsal fin spines, which are followed by pelvic and then pectoral fin rays. All fin rays begin to ossify before their respective supporting structures. Somewhat more detailed descriptions of ossification follow.

In the smallest larva cleared (2.6 mm) the only stained structures are the cleithra and basioccipital. By ca. 4 mm the posterior parasphenotic has begun to ossify; parasphenotic ossification is complete and the exoccipitals begin to ossify at ca. 4.6 mm. Exoccipital ossification is essentially complete and posttemporal ossification is beginning at ca. 5.1 mm. Ossification of the frontal bones initiates at ca. 5.6 mm. The lacrimal ap-

TABLE 1.—Meristics of cleared and stained *Genyonemus lineatus* larvae. Larvae smaller than 4.64 mm are not included since fin rays and vertebrae are not ossified below this size. Specimens between dashed lines are undergoing notochord flexion.

Standard length (mm)	Vertebrae	Caudal rays		Dorsal rays	Anal rays	Pectoral rays	Pelvic rays	Branchiostegal rays (left side)	Gill rakers
		Primary	Secondary						
4.76		4						4	
5.12		4						5	0+0+5
5.56	11	10						7	(not ossified)
6.00	15	13						7	0+0+5
6.12	17	13						7	0+0+5
6.28	18	13						7	0+0+6
6.64	24	17		10	5			7	0+0+9
7.97	25	17	4	XII, 21	I, 11	4		7	3+1+9
10.46	26	17	6	(dam.), 22	II, 11	8	4	7	3+1+12
14.49	26	17	16	XIII, 22	II, 12	17	I, 5	7	4+1+15
32.00	26	17	17	XIV, 21	II, 11	I, 17	I, 5	7	(damaged)

pears at ca. 6.6 mm. By 8 mm additional bones ossified include the epiotic, sphenotic, supraoccipital, parietal, nasal, and the first circumorbital. The skull is essentially complete by ca. 14.5 mm.

None of the bones of the splanchnocranium are ossified at the beginning of the larval stage. By 4 mm they are all ossifying. Teeth first appear at ca. 4.3 mm; four are present on the premaxillary. Four to six dentary teeth are acquired by 5.6 mm; 18 premaxillary teeth are present at this size. Numbers of teeth increase through subsequent larval development: an 8 mm specimen has 26 premaxillary and 18-20 dentary teeth while a 14.5 mm specimen has 60 and more than 30, respectively.

Bones of the suspensorium begin ossifying at ca. 4.2 mm; the hyomandibular and symplectic are first. The ectopterygoid begins to ossify at ca. 6 mm and the quadrate at ca. 6.1 mm. The metapterygoid is next (8 mm). The suspensorium is essentially complete by 14.5 mm.

The opercular apparatus begins ossification at ca. 4 mm with the opercular and preopercular bones. The subopercular is added at ca. 4.2 mm and the interopercle at ca. 4.3 mm. Subsequent development consists of spination and further ossification of these bones.

Ossification of the branchial apparatus commences by 4 mm with the ceratobranchials of the outer two arches. By ca. 4.3 mm the ceratobranchials of four arches are ossified and the hypobranchials are just beginning to ossify. Two pairs of pharyngeal teeth appear at ca. 4.4 mm although the associated pharyngobranchial bones remain unossified until ca. 8 mm. Gill rakers on the outer arch first appear at ca. 5.1 mm—5 lower rakers are present. By 8 mm the number of gill rakers on the outer arch increases to three upper + one at the angle + nine lower rakers. Epibranchials begin to ossify at this size. The basibranchial ossifies between 10.5 and 14.5 mm but the hypohyal remains unossified into the early juvenile stage. The gill raker count at the end of the larval stage is 4+1+15 on the outer arch.

The first three branchiostegal rays are ossifying by 4 mm. A fourth branchiostegal ray and the posterior part of the ceratohyal begin ossification at ca. 4.2 mm; the fifth branchiostegal follows at ca. 4.6 mm. All seven branchiostegals, the epihyal, and interhyal are present by 5.6 mm. Ceratohyal ossification is complete and urohyal ossification is beginning by 6.3 mm. The hyoid apparatus is essentially complete by 14.5 mm, except for the unossified hypohyal.

Vertebral ossification begins with the anterior centra and proceeds posteriorly. Each vertebra ossifies from its ventral midline toward its dorsal midline. Ossification is first evident in a 5.6 mm specimen in the staining of the anterior seven vertebral centra and first four neural arches. In this same specimen centra 8 through 11 are stained ventrally only. By 6 mm the first 10 centra are completely stained, the next 3 on the ventral half only, and the next 2 on the ventral midline only. At this size the first 20 neural arches and 5 haemal arches (originating at the twelfth centrum) are becoming ossified. At 6.3 mm the first 18 centra, 20 neural arches, and 7 haemal arches are stained. By 6.6 mm the anterior part of the urostyle and all except the last centrum are ossified, along with 23 neural arches and 12 haemal arches. The final complement of 25 neural and 14 haemal arches is attained by 8 mm. The first four pleural ribs and three epipleural ribs develop during the transitional period, at ca. 14.5 mm.

The cleithra are the first bones to ossify in the pectoral girdle (by 2.6 mm). The supracleithra begin to ossify at ca. 4.6 mm and the postcleithra at ca. 5.6 mm. The first pectoral radial, coracoid, and scapula begin to stain during the transition to juvenile, after most of the pectoral rays are already ossified. The basipterygia of the pelvic girdle begin to ossify at this time as well.

The general sequence of dorsal and anal fin pterygiophore differentiation is described above under Fin Development. Ossification in both fins begins after 10.5 mm and is completed during the transition to the juvenile stage.

Pterygiophores of the anal spines are fused. Except for the pterygiophores of the first and last soft rays, each successive pair lies between adjacent haemal spines (Fig. 6).

The first two dorsal pterygiophores (bearing the first two dorsal spines) fuse during ossification. The pattern of dorsal pterygiophore placement between adjacent neural spines is somewhat variable (Table 2). Three predorsal bones develop during the transitional period.

The central three hypural elements begin to ossify at ca. 6.1 mm and all hypurals are ossified by 8 mm. These are distinguishable as separate elements throughout larval development. All but one of the principal caudal rays are associated with these elements; the other is associated with the haemal spine of the penultimate vertebra

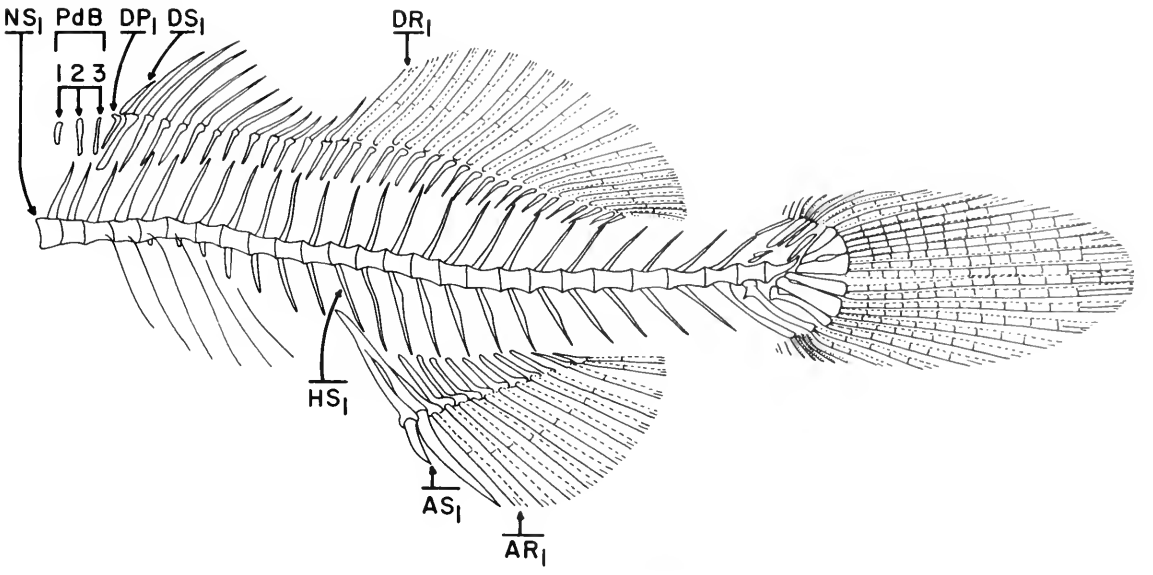

FIGURE 6.—Vertebral column and median fins of a 17.68 mm juvenile *Genyonemus lineatus*, showing typical relationships of dorsal and anal pterygiophores to neural and haemal spines. NS, first neural spine on the first vertebra; PB, predorsal bones; DS, first dorsal spine; DP, first dorsal pterygiophore; DR, first dorsal ray; HS, first haemal spine; AS, first anal spine; AR, first anal ray.

TABLE 2.—Number of dorsal pterygiophores between adjacent neural spines in *Genyonemus lineatus*.

Standard length (mm)	First dorsal pterygiophores	Second dorsal pterygiophores
32	1, 2, 1, 2, 1, 1, 2, 1, 1	1, 2, 2, 2, 2, 3, 2, 3, 2, 3
110	1, 2, 2, 1, 2, 3, 1, 2	2, 2, 2, 2, 2, 2, 2, 3, 2, 1
115	1, 2, 1, 2, 1, 2, 1, 2, 2	1, 2, 3, 2, 2, 2, 3, 2, 3
180	1, 2, 1, 2, 1, 1, 2, 2, 2	2, 2, 2, 3, 2, 2, 3, 3, 1
197	1, 2, 1, 2, 1, 2, 1, 2, 2	2, 2, 3, 2, 1, 3, 2, 3, 1

which is also associated with the first lower secondary caudal ray. Additional lower secondary caudal rays apparently are becoming associated with the haemal spine of the antepenultimate vertebra in specimens larger than 10.5 mm. The first (unossified) epural is associated with the first upper secondary ray at 8 mm. There are five supporting structures above the urostyle in specimens larger than 10.5 mm; the anterior three appear to be associating with the neural spine of the penultimate vertebra, and support five secondary caudal rays. Additional dorsal secondary rays in larger larvae are supported by the neural spine of the antepenultimate vertebra.

Proportions

Larval development of *G. lineatus* is a gradual process without rapid changes in body proportions: all body parts measured are linearly related to standard length through the larval period (Table 3). Since it is of little value to describe such growth only a summary of measurements is given (Table 4).

TABLE 3.—Summary of regressions of measurements of body parts (y) on standard length (x) of *Genyonemus lineatus* larvae.

y	n	r	Regression equation
Head length	164	0.99	$y = -0.24 + 0.32x$
Snout length	155	0.97	$y = -0.10 + 0.09x$
Eye diameter	165	0.98	$y = 0.04 + 0.09x$
Preanal length	166	0.99	$y = -0.51 + 0.59x$
Preanal fin length	85	0.97	$y = 0.20 + 0.62x$
Depth at pectoral insertion	165	0.98	$y = -0.003 + 0.30x$

COMPARISON WITH SIMILAR SPECIES

Genyonemus lineatus eggs closely resemble those of many other fish which spawn in the nearshore coastal waters off southern California. Consequently, separation to the species level is difficult and of doubtful practicality in the routine identification of ichthyoplankton samples.

Among the fish larvae commonly taken in inshore plankton samples along the southern California coast, *G. lineatus* most closely resembles

TABLE 4.—Summary of measurements (in millimeters) of *Genyonemus lineatus* larvae. The mean ($\bar{x}$), sample size (n), and standard deviation (SD) are given for each distance measured. Notochord flexion takes place in the size range demarked by dashed lines.

Size class (SL)	Head length			Snout length			Eye diameter			Preanal length			Preanal fin length			Depth		
	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD	$\bar{x}$	n	SD
[1]1.51-2.00	0.48	12	0.06	—			0.20	13	0.02	.98	13	0.05	—			0.68	13	0.02
[1]2.01-2.50	0.46	10	0.03	0.10	10	0.03	0.20	10	0.01	.99	10	0.02	—			0.54	10	0.07
[2]2.51-3.00	0.49	6	0.03	0.13	6	0.02	0.22	6	0.02	1.04	6	0.06	—			0.54	6	0.06
[3]2.01-2.50	0.54	2	0.03	0.14	2	0.03	0.25	2	0.01	1.16	2	0.11	—			0.74	2	0.08
2.51-3.00	0.59	5	0.08	0.13	5	0.04	0.27	5	0.02	1.11	5	0.12	—			0.78	5	0.78
3.01-3.50	0.69	8	0.08	0.20	8	0.05	0.32	8	0.03	1.41	8	0.11	—			0.91	8	0.07
3.51-4.00	0.85	7	0.05	0.21	7	0.04	0.36	7	0.02	1.61	7	0.13	—			1.07	7	0.09
4.01-4.50	1.09	8	0.15	0.28	8	0.06	0.40	8	0.02	1.98	8	0.19	—			1.22	7	0.11
4.51-5.00	1.26	5	0.08	0.36	5	0.02	0.44	4	0.01	2.22	5	0.08	—			1.36	5	0.04
5.01-5.50	1.43	6	0.14	0.37	6	0.10	0.47	6	0.03	2.32	6	0.18	2.93	3	0.37	1.44	6	0.22
5.51-6.00	1.55	9	0.18	0.42	9	0.07	0.53	9	0.06	2.82	9	0.28	3.32	5	0.22	1.81	9	0.20
6.01-6.50	1.78	7	0.20	0.45	8	0.06	0.59	7	0.06	2.98	8	0.23	3.64	5	0.20	1.86	8	0.11
6.51-7.00	1.94	4	0.09	0.43	4	0.04	0.65	4	0.03	3.38	4	0.08	4.05	3	0.08	2.13	4	0.15
7.01-7.50	2.13	5	0.11	0.55	5	0.08	0.70	5	0.05	3.62	5	0.12	4.40	5	0.19	2.21	5	0.06
7.51-8.00	2.31	5	0.19	0.65	5	0.03	0.72	5	0.09	3.97	5	0.29	4.64	4	0.10	2.35	5	0.18
8.01-8.50	2.40	8	0.15	0.66	8	0.09	0.78	8	0.05	4.19	8	0.26	5.05	7	0.35	2.56	8	0.22
8.51-9.00	2.59	5	0.24	0.72	5	0.10	0.81	5	0.06	4.60	5	0.29	5.26	4	0.10	2.78	5	0.17
9.01-9.50	2.73	5	0.14	0.78	5	0.10	0.85	5	0.05	4.72	5	0.24	5.45	5	0.15	2.78	5	0.23
9.51-10.00	2.95	6	0.11	0.78	6	0.10	0.88	6	0.04	5.13	6	0.38	5.86	6	0.21	2.94	6	0.20
10.01-10.50	3.14	9	0.20	0.78	9	0.09	0.93	9	0.05	5.38	9	0.26	5.92	8	0.23	3.08	9	0.11
10.51-11.00	3.22	6	0.06	0.79	6	0.06	0.95	6	0.07	5.83	6	0.23	6.41	6	0.17	3.22	6	0.06
11.01-11.50	3.40	7	0.12	0.93	7	0.07	1.04	7	0.05	6.20	7	0.20	6.73	7	0.18	3.34	7	0.16
11.51-12.00	3.08	1	—	0.83	1	—	0.82	1	—	6.00	1	—	—			3.50	1	—
12.01-12.50	3.68	2	0.22	1.04	2	0.06	1.10	2	0.04	6.53	2	0.16	7.16	1	—	3.51	2	0.01
12.51-13.00	3.83	4	0.26	1.00	4	0.12	1.05	4	0.09	7.15	4	0.21	7.75	4	0.15	3.75	4	0.16
13.01-13.50	4.00	2	0.06	0.96	2	0.11	1.10	2	0.03	7.38	2	0.25	7.96	2	0	3.62	2	0.37
13.51-14.00	4.08	1	—	1.04	1	—	1.20	1	—	7.64	1	—	8.16	1	—	4.12	1	—
14.01-14.50	4.30	2	0.25	1.10	2	0.03	1.22	2	0.08	8.22	2	0.54	8.52	2	0.28	4.20	2	0.45
14.51-15.00	4.72	1	—	1.40	1	—	1.24	1	—	—			—			—		
15.01-15.50	—			—			—			—			—			—		
15.51-16.00	—			—			—			—			—			—		
16.01-16.50	5.24	1	—	1.56	1	—	1.36	1	—	9.32	1	—	10.04	1	—	4.80	1	—
16.51-17.00	—			—			—			—			—			—		
17.01-17.50	6.48	1	—	1.66	2	0.48	1.80	2	0.17	11.74	2	2.46	12.16	2	2.60	5.82	2	0.76
17.51-18.00	—			—			—			—			—			—		
18.01-18.50	4.84	1	—	1.28	1	—	1.32	1	—	8.48	1	—	8.76	1	—	4.32	1	—
18.51-19.00	5.64	1	—	1.60	1	—	1.48	1	—	11.64	1	—	11.96	1	—	5.64	1	—
19.01-19.50	5.20	1	—	1.52	1	—	1.52	1	—	10.40	1	—	10.80	1	—	5.00	1	—
19.51-20.00	5.52	1	—	1.48	1	—	1.68	1	—	11.36	1	—	11.84	1	—	5.80	1	—

[1]Reared specimens, yolk-sac stage.
[2]Reared specimens, postyolk-sac stage.
[3]Field specimens.

the sciaenids *Seriphus politus* and *Roncador stearnsii* (Moser and Butler[5]), the haemulid *Anisotremus davidsonii*, and the scombrid *Scomber japonicus*. *Genyonemus lineatus* is principally a winter spawner while the other species are principally summer spawners, but some overlap occurs in spring and fall.

Scomber japonicus is distinct in having 30-31 myomeres versus 25-26 for the other species. Yolk-sac larvae of *A. davidsonii* are undescribed; however, yolk-sac larvae of the Atlantic haemulids *Haemulon plumierii* (Saksena and Richards 1975) and *Orthopristis chrysoptera* (Hildebrand and Cable 1930) have an anterior oil droplet in contrast with the posterior oil droplet typical of sciaenids. *Seriphus politus* yolk-sac larvae lack the dorsal pigmentation and banded pattern typical of *G. lineatus* (Moser and Butler footnote 5). *Roncador stearnsii* closely resemble *G. lineatus* until late in the yolk-sac stage (Moser and Butler footnote 5) when *G. lineatus* may be distinguished by a single (rarely two) large dendritic nape melanophore extending into the finfold rather than two or more smaller nape melanophores not extending into the finfold. *Roncador stearnsii* typically has heavier anterior gut pigment than *G. lineatus*.

Characters useful for separating *G. lineatus* from similar larvae are summarized in Table 5. The nape melanophore separates *G. lineatus* larvae from *A. davidsonii* and *S. politus* for as long as it remains visible. *Anisotremus davidsonii* may be distinguished from *G. lineatus* to at least as small as 2.6 mm by ventral pigmentation, and by dorsal fin ray counts in older specimens

[5]H. G. Moser, and J. L. Butler. Description of the early life history stages of croakers (Family Sciaenidae) occurring off California. Manuscr. in prep. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038. Pers. commun. February 1981.

TABLE 5.—Selected characters of larvae which resemble *Genyonemus lineatus*.

Species	Myomeres	Dorsal fin rays	Anal fin rays	Preanal lengths (% of SL) mean (range)	Depth (% of SL) mean (range)	Nape melano-phore	Melanophore above hindgut	Number of midventral trunk melanophores mode (range)
Anisotremus davidsonii	25-26	XI-XII, 14-16	III, 9-11	[1]48 (43-52)	22 (19-25)	No	Large	14 (12-18)
Genyonemus lineatus	25-26	XII-XV+1, 18-25	II, 10-12	[2]47 (38-53)	30 (26-34)	Yes	Small, often absent	Decreases with growth (2-21)
Roncador stearnsii	25-26	IX-X+1, 21-25	II, 7-9	[3]40 (33-49)	24 (18-31)	Yes	Large	Decreases with growth (5-29)
Seriphus politus	25-26	VII-IX+1, 18-21	II, 21-23	[4]46 (40-54)	26 (23-29)	No	Usually present, usually large	Decreases with growth (2-24)
Scomber japonicus	30-31	VIII-XI+1, 9-14+4-6	II, 9-12+4-6	[5]53 (46-59)	25 (23-27)	No	Two or more	[6]Decreases with growth (10-26)

[1]52 specimens, 2.6-8.1 mm SL.
[2]94 specimens, 2.6-9.7 mm SL.
[3]19 specimens, 2.2-4.3 mm SL.
[4]50 specimens, 3.6-9.8 mm SL.
[5]Taken from Kramer 1960, table 5. Larvae 4.00-9.99 mm SL.
[6]20 specimens, 2.2-5.5 mm SL.

(Table 5). *Anisotremus davidsonii* commonly has a uniform row of one midventral, postanal trunk melanophore per myomere after the first postanal myomere, and nearly always has a large melanophore anteriorly on the ventral midline of the gut. As many as four smaller melanophores may also be arrayed along the midline of the gut. *Genyonemus lineatus*, in contrast, rarely displays uniformity in the midventral, postanal melanophore series (those at myomeres 9-10 and 16-18 typically are distinctly larger), and the ventral gut pigmentation usually is not on the midline. *Genyonemus lineatus* is deeper bodied and its hindgut turns down at a much steeper angle than that of *A. davidsonii*.

Seriphus politus lacks the banded pattern of young *G. lineatus* larvae and usually displays an approximately uniform series of small, postanal midventral melanophores (Moser and Butler footnote 5). Shortly before anal anlage development two melanophores of the midventral series typically enlarge in *S. politus*; these lie at myomeres 11-13 and 19-21 versus 9-10 and 16-18 for *G. lineatus*. During anal fin development the anterior of these migrates internally in *G. lineatus* but remains external in *S. politus*. Specimens smaller than 8 mm are often distinguishable by the presence and size of the melanophore above the hindgut (Table 5). The melanophore on the anterior visceral mass also distinguishes these two after it has assumed its ventral position in *G. lineatus*. *Seriphus politus* larvae are somewhat more slender than *G. lineatus*. Anal fin ray counts separate older specimens.

Roncador stearnsii larvae closely resemble *G. lineatus* (Moser and Butler footnote 5). Before acquisition of fin rays *R. stearnsii* may often be distinguished by having rather heavy anterior gut pigmentation (usually light in *G. lineatus*), by the large melanophore above the hindgut, and by one to three pairs of internal melanophores along either side of the midline of the head behind the eye at the level of the floor of the otic capsule plus one or two medially under the forebrain (these often give the appearance of a stripe through the eye, lacking in *G. lineatus*). Dorsal and anal fin ray counts separate older specimens.

DISTRIBUTION

Genyonemus lineatus off southern California spawns principally from October through April (Skogsberg 1939; Goldberg 1976). This is consistent with our study off San Onofre: larvae were taken from January (initiation of our study) through early June 1978, and early October 1978 through late June 1979, with abundance peaks in March 1978 and February 1979 (Walker et al. footnote 2). Few larvae were taken in June or October.

The smallest larval *G. lineatus* were most abundant in the epibenthos (lower 0.5 m) shoreward of about 3.9 km (21 m isobath) and in the water column above the epibenthos between 2 and 3.9 km from shore (13 and 31 m isobaths). During development, they move shoreward and tend to become more strongly epibenthic. This is evidenced by the low abundance of larvae between ca. 3.8 and 6.4 mm in the water column and offshore of 3.9 km. Larvae larger than 6.4 mm are virtually absent above the epibenthos. The abundance peak for *G. lineatus* larvae larger than ca. 3.8 mm is between 1 and 2 km from shore (9 to 12 m isobaths)[6]. Brewer et al. (in press) noted a similar distribution in their study of the

[6]Barnett, A. M., A. E. Jahn, P. D. Sertic, and W. Watson. 1980. Long term spatial patterns of ichthyoplankton off San Onofre and their relationship to the position of the SONGS

ichthyoplankton from the shallow coastal waters of the Southern California Bight.

SUMMARY

1) The *G. lineatus* egg is pelagic, transparent, and spherical with an unsculptured chorion, unsegmented yolk and a single clear to yellowish oil droplet. The live egg averages 0.85 mm in diameter and the oil droplet 0.23 mm. Hatching occurs about 52 h after spawning.

2) Yolk-sac larvae hatch at about 1.8 mm in an undifferentiated state with unpigmented eyes, straight tubular gut, large yolk sac, and posterior oil droplet. Pectoral buds develop during the second day after hatching, the mouth opens and gut begins differentiating on the third, eye pigmentation is complete on the fifth, and yolk exhaustion and swim bladder inflation occurs on the sixth.

3) Yolk-sac larvae initially are pigmented primarily on the dorsum. During the yolk-sac period melanophores migrate toward the ventral midline.

4) Pigmentation is largely restricted to the ventrum and dorsal surface of the gut through much of the larval stage. A nape melanophore and the large internal melanophore on the lower anterior midline of the visceral mass are characteristic. A barred pattern develops during the transition to the juvenile stage.

5) The order of ossification (first uptake of alizarin stain) is: cleithra (2.6 mm); splanchnocranium, hyoid apparatus, opercular apparatus, branchial apparatus, skull (4 mm); caudal fin rays (4.8 mm); vertebrae (5.6 mm); second dorsal and anal fin rays and hypural complex (6 mm); first dorsal and pelvic fin rays (7.2 mm); and pectoral fin rays (7.8 mm). Each fin ray begins to ossify before its supporting structure.

6) The principal characters useful for separating *G. lineatus* from similar larvae are the nape melanophore, the anterior visceral mass melanophore when in its ventral position, the larger midventral melanophores at myomeres 9-10 and 16-18, and fin ray and myomere counts.

7) *Genyonemus lineatus* spawns mainly from October through April, with peak spawning in late winter.

8) Larvae are located principally within 4 km from shore. As they develop they tend to move shoreward and into the lower 1 m of the water column.

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ELEMENTAL COMPOSITION (C,N,H) AND ENERGY IN GROWING AND STARVING LARVAE OF *HYAS ARANEUS* (DECAPODA, MAJIDAE)

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ABSTRACT

Laboratory-reared larvae of the spider crab, *Hyas araneus* L., were studied with regard to their fresh weight (FW), dry weight (DW), carbon (C), nitrogen (N), hydrogen (H), and energy content (J; estimated from C). FW remains fairly constant in each larval stage, regardless of feeding or starving conditions. This is due to regular changes in water content as opposed to those in organic constitutents. FW therefore is not a good measure for living biomass. Growth in fed zoeal stages, if expressed by gain in any parameter but FW, can be described by power functions of time. There is a considerable gain (by a factor of 2 to 3) within each of these two instars. In the magalopa also a high amount of C, N, H, and energy is accumulated, but most of this gain is lost again during the last third of its stage duration. This finding suggests that there is no more food uptake during this last period preceding metamorphosis to the crab. In all larval stages, weight-specific energy (J/mg DW) follows rather a cyclic pattern with decreases before and after molts, and increases during intermolt periods. It shows a decreasing trend during larval development. The loss in cast exoskeletons is <10% of premolt organic matter in the zoeal stages, but >30% in the megalopa. During starvation, biomass declines in an exponential pattern. Larvae of all stages die, when ca. 40 to 60% of their living substance and energy is lost. The C:N ratio suggests that protein serves as the main source of energy; in the final phase, presumbaly, lipids are also catabolized. Weight-specific energy and probably also metabolism decrease in a hyperbola-shaped curve.

Advanced rearing techniques developed in the last three decades have greatly increased our knowledge of autecology and physiology of meroplanktonic marine larvae. However, there is little quantitative information on growth, energetic needs, and reserves.

Within the literature on decapod larvae, there are numerous data on size increments from one developmental stage to the next (Rice 1968), but few on biomass production. Since size is fairly constant in each particular instar, this information represents only a rough measure of actual growth patterns.

A number of authors have investigated biochemical or energetic aspects of larval development in decapod crustaceans: Reeve (1969), Mootz and Epifanio (1974), Frank et al. (1975), Sulkin et al. (1975), Logan and Epifanio (1978), Morgan et al. (1978), Anger and Nair (1979), Capuzzo and Lancaster (1979), Omori (1979), Dawirs (1980), Stephenson and Knight (1980). These studies, however, mainly concentrated on gross differences among larval stages rather than on changes within single instars. Thus, biomass was either considered practically constant in each stage, or it was interpolated by means of (mostly exponential) regression equations describing growth from the first to the last larval instar. The present paper attempts to analyze actual growth patterns within stages of the spider crab, *Hyas araneus*.

Growth achieved in the laboratory under optimal food conditions (as in this paper) probably represents only one end of the scope in which development is possible, rather than a typical expression of it. The other end is characterized by the poorest food level still allowing minimal growth. Anger and Dawirs (1981) discussed the potential ecological role of starvation in a variable environment. They showed that larvae of *Hyas araneus* are well adapted to this condition.

In the present study diminution and growth rates were estimated from frequent samples of starved and fed larvae. They constitute a further step toward a better understanding of larval ecology and energetics in North Sea species as required in a joint research project (Anger and

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Nair 1979; Dawirs 1979, 1980; Anger and Dawirs 1981).

MATERIALS AND METHODS

Ovigerous *Hyas araneus* were dredged from a deep channel near the island of Helgoland (North Sea) during early winter in 1978-79 and 1979-80. After hatching, the zoeae were isolated in vials and maintained individually at 12°C. Food (a mixture of freshly hatched Australian *Artemia* sp. nauplii and the rotifer *Brachionus plicatilis*) and filtered seawater were changed every second day. The methods of obtaining and rearing the larvae have been described in detail by Anger and Dawirs (1981).

For determination of wet weight, larvae were caught individually with pen-steel forceps, briefly rinsed in water from an ion exchanger, blotted for about 10 s on filter paper, and transferred to preweighed silver cartridges. All weight measurements were carried out on an Autobalance AD-2 (Perkin-Elmer)[3] to the nearest 0.1 μg. The techniques and equipment used for obtaining dry weight (DW), carbon (C), nitrogen (N), and hydrogen (H) content of larvae and young crabs were the same as described by Anger and Nair (1979) and Dawirs (1980): deep freezing, vacuum drying, weighing, and combustion in a C-H-N analyzer (Model 1106, Carlo Erba Science). Only rinsing of the material (see above) was added as an initial step. This standard procedure was adopted to remove possible adherent salt and thus to increase the accuracy of the measurements. Comparison of test measurements, however, did not show significant differences (Anger and Nair 1979).

Energy estimates (J) were obtained from carbon values by applying the N-corrected regression equation given by Salonen et al. (1976). Statistical procedures were the same as referred to in detail by Anger and Dawirs (1981). In regression equations, intercept (b) and slope (m) are given; in addition, correlation coefficients (r) and their level of significance (P) for deviation from zero are provided. For logarithmic transformations, ln (= $\log_e$) was applied. All statistical tests were two-tailed.

In May 1979, a first series of 46 analyses comprising 123 individually reared zoea-1 larvae (Z-1) of *Hyas araneus* was carried out to compare their growth patterns with those previously observed by Anger and Nair (1979) in commonly reared zoeae. This set of data showed unsatisfactorily high variation, and high mortality prevented a larger number of analyses. For this reason, in February 1980 another set of 92 analyses comprising 110 prezoeae, 274 Z-1, and 30 early Z-2 was obtained (Table 1). The data for later stages given in Table 2 had been obtained in March and April 1979 (112 samples, 149 individuals).

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

RESULTS

Larval Growth

Fresh weight (FW) values fluctuated around constant levels in all larval stages without clear increase in a single stage (Tables 1, 2). This steplike growth pattern did not allow any analysis of actual body growth during larval instars.

The gain in total live weight (FW) from the prezoea to the freshly metamorphosed crab was ca. 770%. It was 640% in DW, and only ca. 470% in C, N, and H. The absolute increase during larval development is shown in Figure 1. During the extremely short, nonfeeding prezoea stage there was no gain in C, N, H, and energy. Molting to the Z-1 resulted in a minor loss of organic constituents (cast cuticle) and in some uptake of water and salt (Table 1; Fig. 1). During the following instars there was an appreciably absolute increase in all parameters considered. It was generally strongest in the second zoeal stage and, surprisingly, weakest in the megalopa.

The values shown in Figure 1 for Z-1, Z-2, and magalopa form a straight line when arranged in a semilogarithmic scale. This indicates that growth from stage to stage followed an exponential pattern during this period.

The different growth patterns in wet weight (steplike) and DW (gradual) were caused by a combination of these two patterns in the water content of the larvae; during each molt, it suddenly increased, and then it gradually decreased during the molt cycle. This decrease could be expressed as a power function in all larval instars: $\ln (\% H_2O) = b + m \ln (t + 1)$, where b is approximately the logarithm of the initial water content, m is the slope, and t is the time (days from the beginning of a particular stage). All r's for these fitted curves were significantly different from zero ($P<0.001$). The rate of de-

TABLE 1.—*Hyas araneus* larval growth. Fresh weight (FW), dry weight (DW), water content (H_2O), carbon (C), nitrogen (N), hydrogen (H), C:N ratio (C/N, by weight), energy content (Joule, J), number of analyses (*n*), and number of individuals analyzed (*N*). Mean values ±95% confidence intervals.

			Prezoea	Zoea 1														Zoea 2	
	Time (d):		0	0	1	2	3	4	5	6	7	8	9	10	11	12	13	0	1
FW		$\bar{x}$	338	493	537	536	558	563	575	560	583	604	607	618	594	595	606	1,008	1,076
	(μg)	±	9	10	22	28	10	22	26	27	12	10	21	42	26	17	—	48	131
DW		$\bar{x}$	57	65	95	108	122	134	142	141	155	153	166	166	174	167	170	168	189
	(μg)	±	3	1	4	5	5	4	5	7	2	3	6	6	6	6	—	6	10
H_2O	(%)		85.6	86.8	82.4	79.8	78.1	76.1	75.2	74.8	73.5	74.7	72.8	73.2	70.7	71.9	71.9	83.3	82.4
C	(%)	$\bar{x}$	41.9	35.1	32.2	32.0	33.2	34.0	35.8	36.7	36.7	39.3	39.0	40.4	40.5	40.4	40.0	38.7	36.1
		±	0.5	0.3	0.5	0.2	0.5	0.3	0.6	0.5	0.6	0.5	0.4	0.5	0.6	0.8	—	0.8	1.0
	(μg)	$\bar{x}$	23.9	22.9	30.5	34.6	40.6	45.9	50.9	51.8	56.8	60.1	64.6	67.1	70.5	67.5	68.1	65.1	68.1
		±	1.3	0.3	1.9	1.6	1.4	1.2	2.8	2.8	1.2	1.3	3.0	2.3	3.4	3.6	—	1.2	3.6
N	(%)	$\bar{x}$	10.6	8.1	6.7	6.4	6.5	6.4	6.7	7.0	7.2	7.6	7.6	8.1	8.3	8.3	8.3	8.3	7.6
		±	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.3	0.2	0.2	0.1	0.1	0.2	—	0.1	0.2
	(μg)	$\bar{x}$	6.0	5.3	6.4	6.9	8.0	8.7	9.5	9.9	11.0	11.6	12.7	13.4	14.0	14.0	14.2	13.9	14.3
		±	0.3	0.1	0.4	0.3	0.2	0.3	0.4	0.4	0.5	0.1	0.6	0.6	0.5	0.7	—	0.2	0.6
H	(%)	$\bar{x}$	6.6	5.0	4.8	4.7	4.9	5.1	5.2	5.6	5.6	5.9	5.8	6.1	6.3	6.2	6.0	6.1	5.6
		±	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.2	—	0.1	0.2
	(μg)	$\bar{x}$	3.8	3.3	4.5	5.1	6.0	6.9	7.4	7.9	8.6	9.0	9.7	10.1	10.9	10.4	10.6	10.3	10.6
		±	0.2	0.1	0.4	0.2	0.2	0.1	0.4	0.5	0.3	0.3	0.5	0.3	0.6	0.7	—	0.2	0.6
C/N		$\bar{x}$	3.9	4.3	4.8	5.0	5.1	5.3	5.3	5.2	5.2	5.2	5.1	5.0	5.0	4.9	4.8	4.7	4.8
		±	0.1	0.03	0.04	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.05	—	0.1	0.1
J/ind.		$\bar{x}$	0.89	0.79	1.01	1.15	1.37	1.56	1.77	1.82	1.99	2.17	2.33	2.46	2.59	2.48	2.49	2.34	2.37
		±	0.05	0.01	0.06	0.05	0.05	0.04	0.11	0.10	0.05	0.05	0.12	0.08	0.11	0.15	—	0.03	0.14
J/mg DW		$\bar{x}$	15.6	12.1	10.7	10.6	11.2	11.5	12.4	12.8	12.9	14.1	14.0	14.8	14.9	14.8	14.6	13.9	12.6
		±	0.9	0.2	0.2	0.1	0.3	0.2	0.3	0.2	0.3	0.3	0.2	0.03	0.4	0.4	—	0.4	0.5
n (analyses)			11	10	5	5	5	5	5	5	5	5	5	5	5	5	1	5	5
N (individuals)			110	50	25	25	25	25	15	15	15	15	15	15	15	15	4	15	15

TABLE 2.—*Hyas araneus* larval growth. For explanation of abbreviations see Table 1.

		Zoea 2					Megalopa							Crab 1		
Time (d):		0	1	4	8	11	0	4	8	12	16	20	24	0	1	2
FW	$\bar{x}$	994	1,150	1,206	1,011	1,094	2,289	1,861	1,961	2,163	2,496	2,187	1,872	2,926	3,597	4,065
(μg)	±	36	308	236	108	31	236	97	180	461	395	297	153	330	238	577
DW	$\bar{x}$	144	172	253	280	291	333	428	517	576	656	576	450	424	622	902
(μg)	±	7	27	25	25	11	55	88	92	170	57	125	62	87	51	135
H_2O (%)		87.3	86.9	82.7	78.3	79.0	87.3	81.3	79.2	79.0	79.2	79.2	80.6	87.3	85.2	77.8
C (%)	$\bar{x}$	32.2	37.5	35.5	36.8	38.5	35.6	30.4	32.6	31.4	33.2	33.6	31.1	33.5	32.4	29.3
	±	1.2	2.7	1.8	1.2	0.6	2.0	0.9	1.8	3.1	2.2	2.2	2.0	1.7	0.7	3.5
(μg)	$\bar{x}$	46.3	62.8	89.7	103.3	111.9	118.9	130.5	169.8	183.6	218.3	195.0	141.2	137.3	201.1	264.5
	±	2.1	11.2	12.3	12.1	5.5	21.9	29.9	36.5	70.8	28.9	56.1	28.5	26.4	16.1	47.7
N (%)	$\bar{x}$	8.0	8.4	7.6	8.2	8.5	8.2	6.2	7.0	7.1	7.9	7.8	7.0	8.3	7.8	6.4
	±	0.3	0.2	0.3	0.2	0.2	0.5	0.1	0.4	0.5	0.2	0.5	0.3	0.6	0.3	1.1
(μg)	$\bar{x}$	11.6	14.4	19.2	23.0	24.6	27.1	26.5	36.5	41.6	51.9	45.1	31.6	34.9	48.2	57.7
	±	0.2	2.0	2.1	2.3	1.2	4.2	5.6	7.9	14.3	5.5	13.0	5.7	5.5	3.4	11.3
H (%)	$\bar{x}$	4.8	5.7	5.2	5.5	5.7	5.3	4.6	5.0	4.8	5.2	5.2	4.9	4.9	4.9	4.3
	±	0.2	0.2	0.3	0.2	0.1	0.4	0.1	0.4	0.5	0.2	0.4	0.4	0.3	0.2	0.6
(μg)	$\bar{x}$	6.9	9.8	13.2	15.5	16.7	17.8	19.9	26.0	28.0	34.0	30.4	22.1	20.8	30.2	39.1
	±	0.4	1.5	1.9	2.1	1.0	3.4	4.6	6.3	10.6	4.2	8.9	4.5	4.0	2.3	7.3
C/N	$\bar{x}$	4.0	4.4	4.6	4.5	4.5	4.4	4.9	4.6	4.4	4.2	4.3	4.4	3.9	4.2	4.6
	±	0.1	0.2	0.1	0.2	0.1	0.2	0.2	0.2	0.2	0.2	0.1	0.1	0.2	0.1	0.3
J/ind.	$\bar{x}$	1.54	2.20	3.11	3.64	4.02	4.14	4.25	5.70	6.09	7.37	6.63	4.66	4.58	6.71	8.49
	±	0.08	0.42	0.47	0.48	0.22	0.81	1.02	1.31	2.58	1.15	2.10	1.06	0.88	0.54	1.77
J/mg DW	$\bar{x}$	10.7	12.8	12.1	13.0	13.8	12.4	9.9	10.9	10.4	11.2	11.4	10.3	10.9	10.8	9.4
	±	0.6	1.5	0.8	0.6	0.3	1.0	0.4	0.8	1.5	1.1	1.1	0.9	0.7	0.4	1.6
n (analyses)		10	3	11	8	14	9	5	7	5	5	5	7	6	13	4
N (individuals)		41	9	11	8	14	9	5	7	5	5	5	7	6	13	4

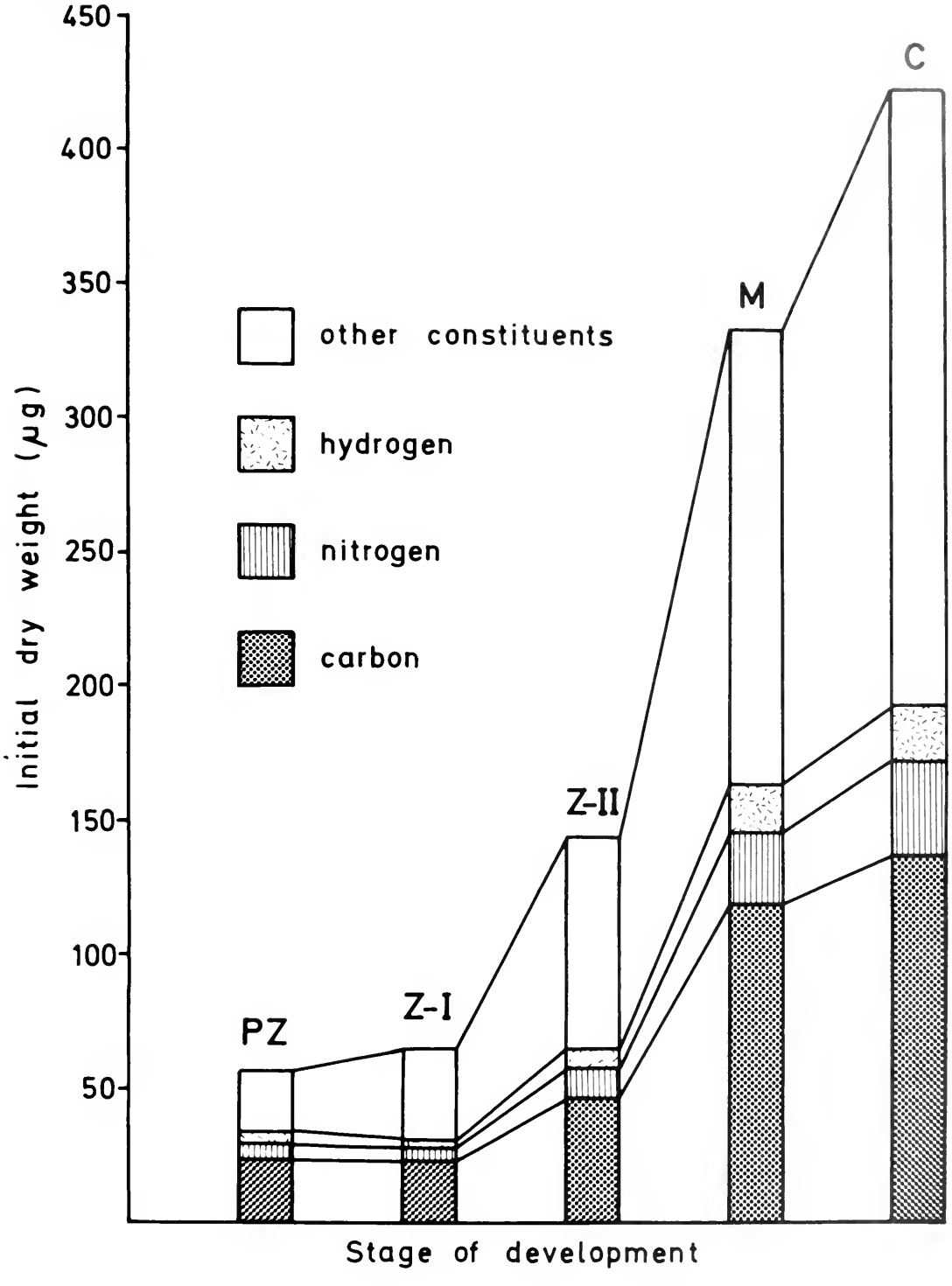

FIGURE 1.—*Hyas araneus*. Initial dry weight, carbon, nitrogen, and hydrogen content in the prezoea (PZ), zoeal stages (Z-I, Z-II), megalopa (M), and first crab stage (C).

crease gradually declined during larval development (Tables 1, 2). This trend was reflected by decreasing m of fitted regression curves: −0.074 in the Z-1, −0.045 in the Z-2, and −0.031 in the megalopa. In Figure 2 only the first regression (Z-1) is shown as the most accurately measured example (the curve for starved zoeae given in the same graph will be discussed below).

Growth in zoeal stages can also be described as a power function of t: $\ln y = b + m \ln(t+1)$, where y is any measure of biomass except FW (DW, C, N, H, J). The b values were almost identical with the logarithms of the initial biomass measure under consideration, the m values varied between 0.29 and 0.48 (Table 3).

The fitted curves describe the actual growth patterns until late premolt was reached. In this very advanced period in the Z-1 stage (days 12 and 13), growth ceased or even switched to a slight loss. These last values were not included in the Z-1 regressions. The fitted growth curves were converted to percentage values of early postmolt levels, so that direct comparison of relative increase rates became possible (Fig. 3; Z-1 curves for 1980 values only).

In zoeae the individual energy content (J) revealed the strongest increment, DW the weakest. The rate of increase in N was similar to that in DW, whereas C and H increased at a higher rate during individual growth (Table 3). A comparison of the biomass values in first zoeae obtained in two different seasons and years shows that the 1979 larvae were not only less viable (see above), but also showed lower initial biomass (reflected by lower b values in all regression equations describing growth) and lower growth rates (reflected by m values), especially in C, H, and J.

TABLE 3.—Parameters of regression equations for individual growth in larval stages of *Hyas araneus*: $\ln y = b + m \cdot \ln(t+1)$. t = time (d); r = correlation coefficient; df = degrees of freedom; dry weight (DW), carbon (C), nitrogen (N), hydrogen (H) in μg, and energy contents (J).

Stage	y	b	m	r	df
Zoea I[1]	DW	4.164	0.300	0.924	44
Zoea I	DW	4.228	0.385	0.989	64
Zoea I[1]	C	2.918	0.370	0.873	44
Zoea I	C	3.107	0.451	0.994	64
Zoea I[1]	N	1.495	0.331	0.839	44
Zoea I	N	1.604	0.384	0.979	60
Zoea I[1]	H	1.016	0.354	0.833	44
Zoea I	H	1.164	0.475	0.994	62
Zoea I[1]	J	−0.511	0.377	0.870	44
Zoea I	J	−0.292	0.479	0.990	64
Zoea II	DW	4.986	0.290	0.938	44
Zoea II	C	3.858	0.354	0.934	44
Zoea II	N	2.449	0.305	0.938	44
Zoea II	H	1.961	0.350	0.925	44
Zoea II	J	0.457	0.381	0.927	44

[1]1979 observation (all others from 1980).

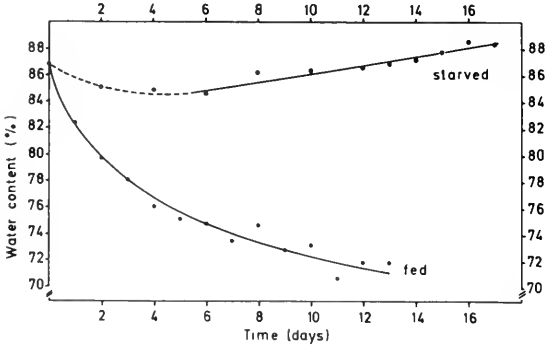

FIGURE 2.—*Hyas araneus*. Water content (% fresh weight) in Z-1 larvae fed and starved for different lengths of time.

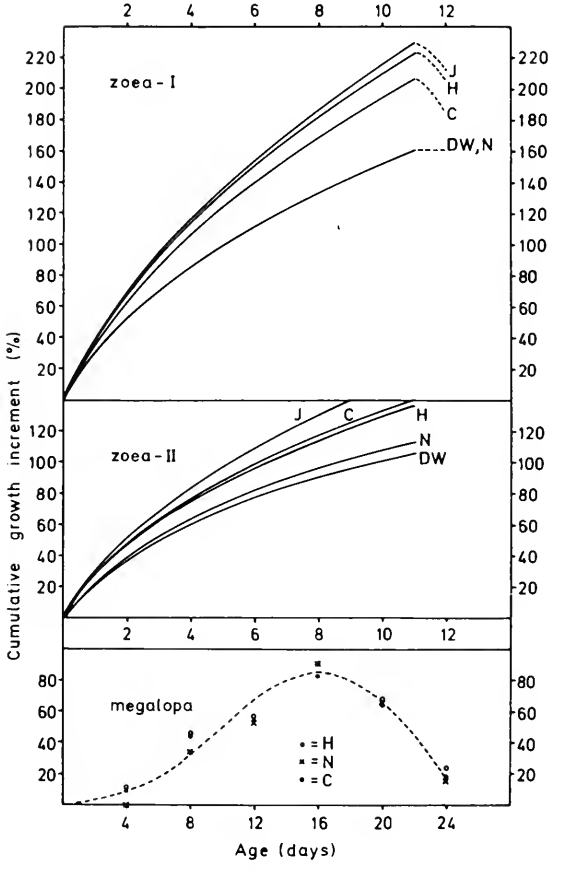

FIGURE 3.—*Hyas araneus*. Growth patterns [dry weight (DW), energy contents (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in all larval stages expressed as percentage of early postmolt levels. Solid curves: fitted by equations (see text); dotted curves: fitted by eye.

However, due to high variation among the 1979 samples, these differences were not statistically significant.

In May 1979, eight Z-2 of *H. araneus* were isolated from a plankton sample and analyzed for comparison. The results (Table 4) compared favorably with those of late laboratory-reared Z-2 larvae (Table 2), although C and H values were slightly higher in the field-caught larvae.

It becomes obvious from Figure 3 (lower graph) that growth in the megalopa was quite different from that in the zoeal stages. Since variation among analyses (see Table 2) was rather high, calculation of fitted growth curves was not considered useful and, therefore, only the assumed pattern was displayed in the diagram as an eye-fitted curve. A surprising decrease in all parameters was found during the last third of the megalopa stage. As a result, young crabs contained only little more organic substances than young megalopae (Fig. 1).

From the above results, approximate average daily energy gains per individual (J/d per ind.) can be calculated. In the 1979 Z-1 larvae a value of 0.08 was estimated. This compares favorably with the data reported by Anger and Nair (1979). They found 0.06 (their figures −0.4 and 0.6 on page 51 are erroneous; they should read −0.04 and 0.06), based on C contents, and 0.07 to 0.11, based on biochemical composition (excluding and including chitin, respectively). Since the 1980 larvae grew better (see above), their daily energy gain was higher: 0.16 J/d per ind. In the second zoeal stage a value of 0.22 was found (Fig. 1). In the megalopa it was similar (0.20) until day 16, when it dropped to −0.34 until metamorphosis; on the average, a weak gain (0.02 J/d per ind.) resulted.

TABLE 4.—Ranges and arithmetic means ($\bar{x}$) for *Hyas araneus* zoea-2 from Helgoland plankton in May 1979. Four analyses comprising eight individuals. For explanation of abbreviations see Table 1.

		Range	$\bar{x}$
FW	(µg)	1,162-1,292	1,220
DW	(µg)	304-346	322
H_2O	(%)	72.6-74.4	73.6
C	(%)	35.0-36.9	35.7
	(µg)	106.7-127.4	115.2
N	(%)	7.60-7.73	7.67
	(µg)	23.1-26.7	24.7
H	(%)	5.23-5.51	5.36
	(µg)	15.9-19.0	17.3
C/N		4.53-4.77	4.66
J/ind.		3.67-4.49	4.00
J/mg DW		12.1-13.0	12.4

The weight-specific energy content (J/mg DW) followed a cyclic pattern (Fig. 4). Due to salt uptake, it decreased during molt, and then it increased again during growth. From instar to instar there was a conspicuous decreasing trend. It was related to a decrease in the percentage of organic substances, expressed as maximum sum of the C, N, and H portions (upper part of Fig. 4).

The ratio between single elements can be used as an index for biochemical composition. Changes in the C:N ratio mainly indicate shifts in the relative amounts of lipids (plus carbohydrates) and proteins (plus free amino acids) (Fig. 5). There were no major differences found during the molt cycles. In all larval stages there was an initial increase, followed by a decline.

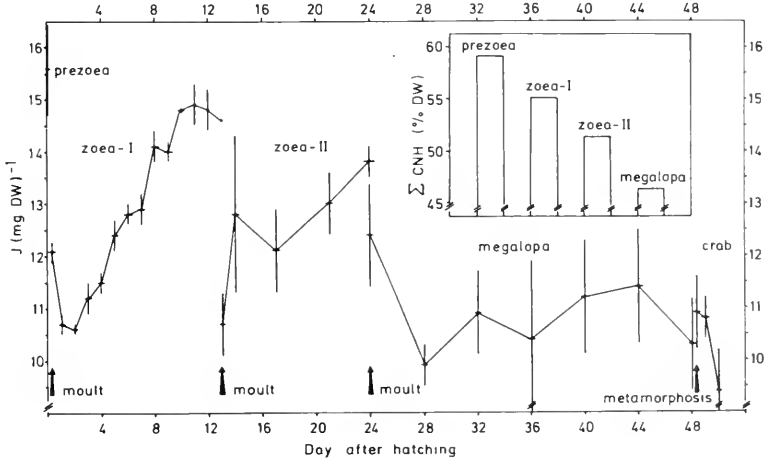

FIGURE 4.—*Hyas araneus*. Changes in weight-specific energy during larval development; vertical lines: 95% confidence intervals of the means. Upper right: Maximum sum of carbon (C), nitrogen (N), and hydrogen (H) in all larval stages.

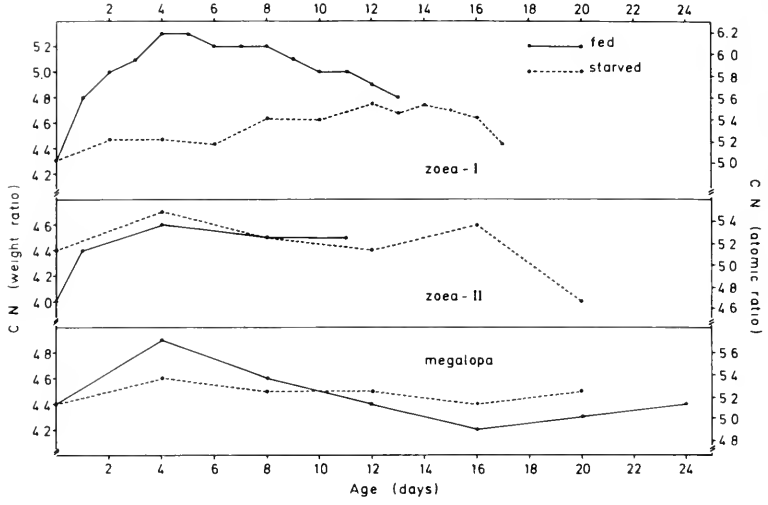

FIGURE 5.—*Hyas araneus*. C:N (carbon:nitrogen) ratio in larvae fed and starved for different lengths of time.

Certainly the buildup of the chitin cuticle, and perhaps also the disproportionately strong storage of lipids, contributed to the increase. The subsequent decrease in the C:N ratio suggests that more proteins than other organic constituents were accumlated later. This trend was best visible in the Z-1 and megalopa stages; in the latter it was followed by a new increase beginning on day 16. This period was identical with that of decreasing biomass (Fig. 3). The curves given in Figure 5 for starved larvae will be discussed below.

The C:H ratio remained fairly constant within stages, and it did not differ much among larval instars. The mean values and 95% confidence intervals (weight-based) were 6.67±0.08 in the Z-1 (1980), 6.64±0.26 in the Z-2, and 6.49±0.11 in the megalopa. In field-caught Z-2 larvae and in young crabs mean ratios of 6.66 and 6.67 were found. The ratios in the Z-1 and megalopa stages were statistically different from each other ($P<0.01$). There was also a significant difference ($P = 0.002$) between the figures in the Z-1 from 1979 (6.86±0.09) and from 1980 (see above).

The growth patterns described in Figure 3 do not consider losses due to shedding of exuviae. In order to determine the approximate amount of organic substances cast during molts, occasional analyses of exuviae were carried out (Table 5). Wet weight and DW measurements did not provide useful results, because the amount of water and salt inside the cast could not be accurately determined. The composition of the exuviae corresponded closely to that of its main component, chitin. Deviations from the theoretical atomic ratio C:N:H = 9:1:14 can partly be explained by analytical inaccuracies (see 95% confidence limits in the megalopa), partly by other biochemical components of exuviae, or by slight chemical changes before sampling and analyzing the casts (partial decomposition).

The amount of organic matter lost during zoeal molts was far lower than during metamorphosis to the crab: 4 to 5% versus 19% in N, 6 to 9% versus 29% in both C and H (Table 5). Assuming an energy content of ca. 18 J/mg dry organic exuvial matter (after Winberg 1971, somewhat corrected for protein compounds) and a C content of ca. 45% (according to the molecular formula of chitin), then the energy losses should be ca. 0.23 J in the Z-1, 0.29 in the Z-2, and 1.61 in the megalopa. These estimates correspond to ca. 9, 7, and 34% of total body energy levels in late premolt in these stages. Compared with average daily energy fixation rates (see above), these figures mean losses of ca. 1.3 to 1.4 d in the zoeal stages, and ca. 8 d in the megalopa.

Preliminary experiments were carried out to

TABLE 5.—Composition [carbon (C), nitrogen (N), hydrogen (H)] of larval exuviae of *Hyas araneus* and percentage of premolt matter cast at ecdysis. n = number of analyses, N = number of exuviae analyzed.

		C (μg)	N (μg)	H (μg)	Weight ratio	Atomic ratio	n	N
Zoea-I		5.85	0.67	0.92	8.7:1:1.4	10:1:19	1	15
% cast		9	5	9				
Zoea-II		7.20	1.10	1.10	6.6:1:1	8:1:14	1	10
% cast		6	4	7				
Megalopa	$\bar{x}$	40.56	5.46	6.39	7.5:1:1.2	9:1:16	7	7
	±	4.07	0.62	0.56				
% cast		29	17	29				

determine food consumption in the Z-1 stage using *Artemia salina* nauplii as prey. The average values found were near 20 μg C/d per ind. or 0.8 to 0.9 J/d. Gross growth efficiency therefore should be about 10 to 20%. The amount taken up by the larvae (3 d old) corresponded to ca. 55% of their own body C and to ca. 36% of their own DW. In light of the experimental conditions, we consider this near the maximum level.

Loss of Biomass During Starvation

FW of starving larvae did not show significant changes (Tables 6 to 8). Also water content could not always be measured with sufficient accuracy to detect clear trends. In the Z-1 and in the megalopa, first a slight decrease and later a conspicuous increase of water content occurred. The latter trend was linear in the Z-1 (Fig. 2); it could

TABLE 6.—*Hyas araneus* losses in starved Z-1 larvae. For explanation of abbreviations see Table 1.

Time (d):		0	2	4	6	8	10	12	13	14	15	16	17
FW	$\bar{x}$	493	538	522	501	534	533	532	557	547	577	584	589
(μg)	±	10	16	27	20	16	29	38	14	28	52	35	39
DW	$\bar{x}$	65	80	79	77	74	73	71	73	70	70	66	68
(μg)	±	1	2	3	3	3	2	2	3	1	2	1	4
H_2O (%)		86.8	85.1	84.9	84 6	86.2	86.4	86 6	86.9	87.2	87.8	88 6	88 4
C (%)	$\bar{x}$	35.1	27.5	25.8	24.7	24.6	23.2	22.8	22 0	22.2	21.7	22.1	21 4
	±	0.3	0.4	0.3	0.2	0.3	0.4	0.6	0.3	0.3	0.4	0.3	1 0
(μg)	$\bar{x}$	22.9	21.9	20 4	19.0	18.2	16.8	16.2	16.1	15 6	15 3	14 6	14 6
	±	0.3	0.2	0.7	0.7	0.8	0.5	0.8	0.8	0 2	0.5	0 4	0.7
N (%)	$\bar{x}$	8.1	6.2	5.8	5.57	5.3	5.0	4.8	4.72	4.7	4 6	4 8	4 8
	±	0.1	0.1	0.1	0.04	0.2	0.2	0.2	0.05	0 1	0.1	0.1	0.2
(μg)	$\bar{x}$	5.3	4.91	4 6	4.3	3.9	3.6	3.4	3.4	3.30	3.26	3 16	3.3
	±	0.1	0.04	0 1	0.2	0.2	0.1	0.2	0.1	0.06	0.07	0.03	0.1
H (%)	$\bar{x}$	5.0	3.82	3.55	3.60	3.33	3.27	3 15	3.11	3.17	3.3	3 2	3.0
	±	0.1	0.05	0.05	0.04	0.04	0.07	0.11	0.06	0.02	0.3	0.1	0 4
(μg)	$\bar{x}$	3.3	3.05	2.8	2.8	2.5	2.4	2 2	2.3	2.23	2 2	2.1	2.1
	±	0.1	0.02	0.1	0.1	0.1	0.1	0.1	0.1	0.02	0.1	0.1	0.1
C/N	$\bar{x}$	4.31	4.47	4.47	4 43	4.63	4.62	4.75	4.67	4 74	4.70	4.64	4.43
	±	0.03	0.04	0.04	0.06	0.12	0.10	0.11	0.09	0.07	0.05	0.11	0.05
J/ind.	$\bar{x}$	0.79	0.69	0.62	0.57	0.55	0.50	0.48	0.47	0.45	0 44	0.42	0 42
	±	0.01	0.01	0.02	0.02	0.02	0.01	0.02	0.02	0.01	0.02	0.01	0.02
J/mg DW	$\bar{x}$	12.1	8.6	7.9	7.4	7.4	6.8	6.7	6.4	6.5	6.3	6 4	6 1
	±	0.2	0.3	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0 4
n (analyses)		10	5	5	5	5	5	5	5	5	5	5	3
N (individuals)		50	25	25	25	25	25	25	25	25	25	25	13

TABLE 7.—*Hyas araneus* losses in starved Z-2 larvae. For explanation of abbrevations see Table 1.

Time (d):		0	4	[1]4	8	[1]8	12	[1]12	16	20
FW	$\bar{x}$	1,150	2,422	1,219	1,184	1,176	1,034	1,022	929	1,240
(μg)	±	308	349	68	102	67	144	—	263	474
DW	$\bar{x}$	172	174	195	145	170	154	172	153	131
(μg)	±	28	14	15	17	24	12	—	17	14
H_2O (%)		85.0	92.8	84.0	87.8	85.5	85.1	83.2	83.5	89.4
C (%)	$\bar{x}$	36.5	29.9	30.4	28.2	27.2	26.7	26.6	25.5	22 2
	±	2.7	1.2	1.9	1.4	1.7	2.2	—	1.4	2.1
(μg)	$\bar{x}$	62.8	52.1	59.6	40.8	46.5	41.1	45.6	39.0	29.0
	±	11.2	6.0	8.1	5.6	9.0	5.6	—	5.9	5.4
N (%)	$\bar{x}$	8.4	6.4	7.0	6.3	6.4	6.1	6.3	5.6	5.5
	±	0.3	0.3	0.7	0.8	0.3	0.1	—	0.3	0 4
(μg)	$\bar{x}$	14.4	11.1	13.5	9.1	10.9	9.7	10.9	8.6	7 2
	±	1.9	1.3	2.2	1.9	1.9	0.9	—	0.9	1.3
H (%)	$\bar{x}$	5.7	4.3	4.2	3.9	3.7	3.8	3.8	3.7	3.1
	±	0.3	0.2	0.4	0.4	0.3	0.4	—	0.2	0.4
(μg)	$\bar{x}$	9.8	7.5	8.2	5.6	6.3	6.2	6.5	5.6	4.1
	±	1.6	0.8	1.3	1.0	1.3	0.8	—	0.8	0.9
C/N	$\bar{x}$	4.4	4.7	4.4	4.5	4.3	4.4	4.2	4 6	4.0
	±	0.3	0.1	0.3	0.5	0.3	0.4	—	0.3	0.1
J/ind.	$\bar{x}$	2.2	1.7	1.9	1.3	1.4	1.3	1.4	1 2	0.8
	±	0.4	0.2	0.3	0.2	0.3	0.2	—	0.2	0.2
J/mg DW	$\bar{x}$	12.8	9.6	9.9	8.9	8.5	8 2	8.2	7.8	6 4
	±	1.0	0.6	0.9	0.6	0.7	1.0	—	0 6	0.8
n (analyses)		3	5	5	5	5	5	2	5	5

[1]Analyses of group maintained larvae.

TABLE 8.—*Hyas araneus* losses in starved megalopa larvae. For explanation of abbreviations see Table 1.

	Time (d):		0	4	8	12	16	20
FW		$\bar{x}$	2,289	2,131	1,963	2,200	2,275	2,370
	(μg)	±	236	192	268	280	158	406
DW		$\bar{x}$	333	327	309	358	304	281
	(μg)	±	55	55	74	103	96	106
H_2O	(%)		85.4	84.7	84.3	83.7	86.6	88.2
C	(%)	$\bar{x}$	35.6	25.8	23.3	23.1	23.0	22.8
		±	2.0	0.6	1.0	1.2	1.6	1.1
	(μg)	$\bar{x}$	118.9	84.7	72.2	83.1	70.5	64.0
		±	21.9	16.3	17.9	27.7	26.8	26.7
N	(%)	$\bar{x}$	8.2	5.6	5.1	5.1	5.2	5.1
		±	0.5	0.3	0.3	0.1	0.3	0.3
	(μg)	$\bar{x}$	27.1	18.4	15.9	18.4	15.9	14.2
		±	4.2	3.6	3.8	5.6	5.2	4.6
H	(%)	$\bar{x}$	5.3	3.7	3.4	3.5	3.3	3.5
		±	0.4	0.2	0.2	0.3	0.2	0.3
	(μg)	$\bar{x}$	17.8	12.0	10.5	12.6	10.2	9.8
		±	3.4	2.5	2.7	4.5	3.7	4.7
C/N		$\bar{x}$	4.4	4.6	4.5	4.5	4.4	4.5
		±	0.2	0.2	0.1	0.2	0.3	0.5
J/ind.		$\bar{x}$	4.1	2.6	2.1	2.4	2.1	1.9
		±	0.8	0.5	0.5	0.9	0.8	0.8
J/mg DW		$\bar{x}$	12.4	7.9	6.9	6.8	6.8	6.7
		±	1.0	0.3	0.4	0.5	0.6	0.4
n (analyses)			9	5	5	5	5	3

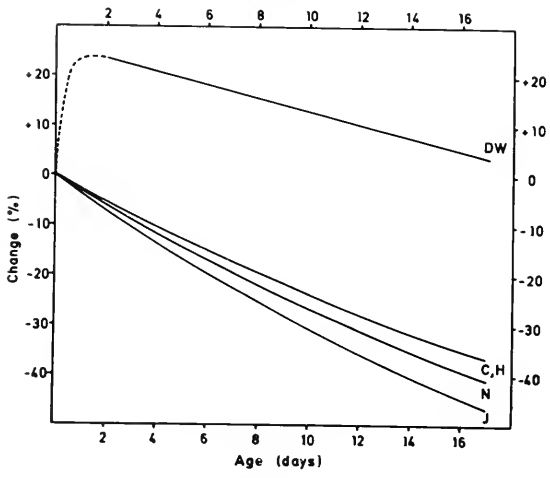

FIGURE 6.—*Hyas araneus*. Loss patterns [dry weight (DW), energy content (J), carbon (C), nitrogen (N), and hydrogen (H) per individual] in starved Z-1 larvae. Solid lines: fitted by equations (see text); dotted curve: fitted by eye.

be expressed by the statistically significant regression equation: $\%H_2O = 83 + 0.32\ t$ ($r = 0.959$; $P<10^{-4}$), where t = time (days from hatching). This effect was visible by eye: larvae, which had starved for a long time, acquired an increasingly bloated appearance like those exposed to a hypotonic medium.

DW tended to decrease during starvation, but due mostly to high variation among parallel determinations, only in the Z-1 stage could a statistically significant trend be found between days 2 and 17 (Fig. 6): DW (μg) = $82 - 0.85\ t$ ($r = 0.966$; $P<10^{-5}$).

The decreases in C, N, H, and J during t followed an exponential pattern: $\ln y = b + mt$, where y is any measure for biomass (C, N, H in μg) or energy (J). To allow direct comparison, fitted curves were again converted to percentage values and shown in Figure 6 (only Z-1 stage as an example). For the other stages similar curves were obtained (Table 9). The slope parameters (= regression coefficients, m, in the log-transformed equations) were not statistically significantly different from each other. The b values were very close to the logarithms of the initial figures for biomass.

In all three larval instars the energy content (J/ind.) dropped more drastically than C, N, and H contents (Table 9). In the Z-1 there was also a slightly stronger decline in N as compared with C and H (Fig. 6). The maximal losses observed shortly before starvation death of the larvae were ca. 36 to 46% in the Z-1, 45 to 58% in the Z-2, and 43 to 51% in the megalopa.

TABLE 9.—Parameters of regression equations for loss of individual biomass in starved larval stages of *Hyas araneus*: $\ln y = b + mt$; t = time (d). For further explanation see Table 3.

Stage	y	b	m	r	df
Zoea I	C	3.127	−0.028	−0.986	61
Zoea I	N	1.653	−0.032	−0.984	61
Zoea I	H	1.167	−0.027	−0.972	61
Zoea I	J	−0.285	−0.037	−0.981	61
Zoea II	C	4.082	−0.033	−0.868	25
Zoea II	N	2.548	−0.029	−0.836	25
Zoea II	H	2.166	−0.036	−0.843	25
Zoea II	J	0.698	−0.041	−0.886	25
Megalopa	C	4.663	−0.028	−0.634	32
Megalopa	N	3.181	−0.030	−0.673	32
Megalopa	H	2.748	−0.029	−0.608	32
Megalopa	J	1.268	−0.038	−0.698	32

The average daily energy loss per individual increased from the first to the last larval stage. If converted to weight-specific figures, a weak opposite trend became visible. This means that increasing reserves became available during the progress of development, and weight-specific metabolism tended to decrease somewhat. However, the above average values are only rough estimates, since the loss patterns are nonlinear (see above), but they do reflect general differences among stages (Table 10).

The decrease pattern in weight-specific energy contents of starved larvae (within stages) followed a hyperbola: $\ln$ J/mg DW $= b + m \ln(t + 1)$, where t = time (days), b is close to the logarithm of the initial value, and m is the slope.

TABLE 10.—Average daily energy loss in starved larval stages of *Hyas araneus* (estimated from carbon-hydrogen-nitrogen values). J = energy contents; DW = dry weight.

Stage	J/d per ind.	J/d per mg DW
Zoea I	0.02	0.35
Zoea II	0.07	0.32
Megalopa	0.11	0.28

The b values of the fitted curves were ca. 2.5, the m's were −0.20 (Z-2) to −0.23 (Z-1); and the r's varied between −0.964 ($P<0.002$; Z-2) and −0.992 ($P<10^{-10}$; Z-1).

Using the conversion factor 20.19 J/ml O_2 given by Brody (1945), approximate figures for oxygen consumption could be estimated from the energy values in Tables 6 to 8. In all stages there was apparently a drastic reduction in respiration rate during the first few days of starvation (Table 11). For comparison of the stages, again average values were computed (from values in Table 10). Corresponding to the weight-specific energy values (see above), from which they were derived, a weak decreasing trend became apparent (Table 11).

The C:N ratio (Fig. 5) did not follow a uniform pattern in starved larvae. In the Z-1 stage a long period of gradual increase was followed by a short period of rapid decrease. This suggests that protein was catabolized at a higher rate than other constituents during most of the starvation period; only in the premortal phase, were N-poor substances (most probably lipids) apparently used as the main energy source. In the Z-2 and in the megalopa variation was too high to discern clear trends. In the former instar the C:N ratio also showed a drop at the end suggesting some similarity with the Z-1, whereas in the latter stage apparently it did not change at all.

The C:H ratio was practically constant in all larval instars. It was in most cases significantly lower in fed than in starved larvae. The mean values and 95% confidence intervals (by weight) were 6.67±0.08 versus 7.07±0.012 in the Z-1 ($P<10^{-5}$), 6.64±0.26 versus 6.98±0.30 in the Z-2 (not significant), and 6.49±0.11 versus 6.80±0.28 in the megalopa ($P=0.014$). There was a similar statistically significant difference ($P = 0.002$) between the C:H ratios found in Z-1 larvae in May 1979 (6.86±0.09) and in February 1980 (6.67±0.08).

TABLE 11.—Weight-specific respiration rates (µl O_2/h per mg dry weight) in relation to the time of starvation of *Hyas araneus*.

Stage	Days of starvation				
	2	4	8	>8	$\bar{x}$[1]
Zoea I	3.6	0.7	0.3		0.73
Zoea II		1.6	0.4		0.66
Megalopa		2.3	0.5	0.2	0.59

[1]Computed from Table 10 data.

DISCUSSION

Larval growth has been measured and described in a number of different ways. Increments in zoeal body size obey the general rules summarized by Rice (1968), who calculated an average growth factor of 1.29 for brachyurans. From the figures given by Christiansen (1973) for *H. araneus*, factors of 1.26 to 1.30 can be derived, depending on the distance measured. A factor of 1.3 is also obtained, if size is assumed to be proportional to the cube root of DW. As pointed out by Rice (1968), the megalopa can hardly be included in those considerations because of its different shape.

It is generally accepted that FW is a poor measure of actual biomass. Its determination is inaccurate and thus yields highly variable results. Moreover, it does not change in an orderly manner during the molt cycle and therefore, it must be regarded as insensitive to changes in organic matter. This is caused by changes in the water content. It is difficult to understand why a number of authors described biochemical and physiological changes in developing crustacean larvae on a wet weight basis, and so severely reduced the value of their information. We suggest that FW or Formalin wet weight never be used as a reference base in such studies, but only as a source of additional information (e.g., for water content of tissues).

DW is a far better measure of biomass, although it is influenced by inorganic salts. Unfortunately, different drying methods (temperatures and times) are used by different investigators. Ash-free DW should improve the accuracy in physiological studies, if used as a basic unit. However, again drying and combustion temperatures and times are not uniformly applied.

Elemental composition, especially C content, can be used as a reliable expression of living organic substance. Inorganic C does not play a signficant role in marine planktonic organisms (Curl 1962) and therefore C is also a measure of energy equivalents (Salonen et al. 1976). C-based energy estimations apparently tend to be somewhat lower than those calculated from bio-

chemical composition (Anger and Nair 1979); comparison of both methods with direct calorimetry in identical material should be worthwhile. However, the J values given in this paper compare favorably with those reported elsewhere for decapod larvae (e.g., Cummins and Wuycheck 1971; Mootz and Epifanio 1974; Logan and Epifanio 1978; Capuzzo and Lancaster 1979; Dawirs 1980; Stephenson and Knight 1980).

The interpretation of changes in the relative chemical composition of larvae (C:N, C:H) leads to interesting assumptions about physiological processes, but there is a need for complementary biochemical investigations. Such analyses are planned for future studies as an extension of the present results. So far, our figures compare favorably with those given in the literature (Childress and Nygaard 1974; Ikeda 1974; Omori 1979; Dawirs 1980). Ikeda (1974) investigated a large number of zooplankton species, and he found that C:N (by weight) is in most cases 3 to 5, whereas C:H is mostly 6 to 7.

Growth (any measure except size and FW) during larval development in decapod crustacea usually follows—at least for some period—an exponential pattern, if gain from stage to stage is considered (Reeve 1969; Mootz and Epifanio 1974; Logan and Epifanio 1978; Johns and Pechenik 1980; Stephenson and Knight 1980). This also holds true for the zoeal stages of *Hyas araneus*. Interpolation of biomass values within single stages from such exponential curves yields poor correspondence of predicted and observed data, because growth within stages follows different patterns. In both zoeae it could be described most accurately by power functions, whereas exponential regressions do not fit as well. At the end of the molt cycle, however, such parabola-shaped fitted growth curves lose their applicability. This final period probably corresponds to the stages D_2 to D_4, during which molt is prepared by separating the epidermis from the old cuticle (Freeman and Costlow 1980). Possibly, there is no more significant food uptake during this phase of body reconstruction (Anger and Dawirs 1981).

In the megalopa, another growth pattern was found. The period of body reconstruction and of presumed inability to take up food preceding metamorphosis appears to be much longer in this stage. The daily energy loss per individual was three times higher during this time as opposed to megalopae starved from the beginning. This contrast suggests that a final fasting period is a normal part of the development program, not considered starvation, and thus not counterbalanced by reduced metabolism. This assumption is supported by a number of observations in other decapod megalopae (Mootz and Epifanio 1974; Schatzlein and Costlow 1978; Dawirs 1980; for recent review see Anger and Dawirs 1981).

The duration of the megalopa stage is much more variable than the zoeal instars. This fact may be related to the ecological role of the megalopa which is to select a biotope suitable for adult life. The capacity to delay selection should be related to the amount of reserve accumulated prior to the change in energy balance. This strategy is in contrast to that observed by Pechenik (1980) in gastropod larvae. These do not cease to grow with the onset of metamorphic competence, and their capability to delay metamorphosis appears to be related to the preceding growth rate. More detailed investigations on the nutritional and ecological needs of the megalopa stage are necessary for a better understanding of this critical phase in benthic recruitment.

All these complicated changes of biomass as well as their extent (two- to threefold increases within single stages) suggest that the use of "characteristic" values for particular instars applied in energy budgets and other energetic considerations must lead to very rough figures.

Another complicating factor is annual or seasonal variation in initial biomass of hatching larvae and in their growth rate. Since viability also appears to be related to this kind of variation, future studies will have to examine its degree and significance. The same holds true for possible systematic differences between laboratory-reared larvae and those obtained from wild plankton. Several authors (Knight 1970 and earlier papers; Rice and Provenzano 1970; Ingle and Rice 1971) observed higher growth rates in naturally grown developmental stages of different decapod species.

Only a small part of the organic matter accumulated during the zoeal stages is lost in exuviae. This is much different in the megalopa. More than three times more matter and energy was found in its cast exoskeleton than in both zoeae combined. These and other striking dissimilarities between zoea and megalopa larvae underline their different roles. The former accumulate energy-rich substances taken from the pelagic food web, and they are responsible for dispersal of the species. The latter stage, which

often crawls on the bottom, presumably will test suitable benthic habitats, before it goes through metamorphosis at a selected site. It appears that a rigid exoskeleton is advantageous as a protective means in the evolution of benthic crustaceans, whereas in pelagic species and stages it is probably disadvantageous for energetic reasons (increasing swimming energy).

The preliminary determinations of feeding rates on *Artemia sp.* nauplii yielded almost the same values (in C per day) as observed by Anger and Nair (1979) using *Polydora ciliata* larvae as prey. This confirms that the amounts in the above data are correct, but further studies considering the whole molt cycle in each larval stage will be necessary for comparisons with the growth measurements of the present investigation. The feeding rates observed in the Z-1 of *H. araneus* as well as larval DW are similar to those found by Mootz and Epifanio (1974) in the Z-4 stage of *Menippe mercenaria.*

Measuring the loss of organic matter and energy during starvation bears the same technical problems as measuring growth. FW, apart from its inaccuracy, is practically constant even during long-term starvation. This masking of changes in organic constituents is again caused by changes in water content. We assume that the underlying mechanism is some kind of starvation edema. Due to degradation of amino acids, the osmotic pressure in the hemolymph must decrease, and consequently water may passively enter body tissues. The water lost in the hemolymph might be replaced by seawater. This assumption would explain the observed net increase in body volume, water, and ash contents of starving larvae (Ikeda 1971, 1974; Mayzaud 1976). Instrusion of inorganic salts replacing degraded organic ions presumably is responsible not only for increasing ash portions, but also for the low degree of loss in DW. The latter observation means that DW can also be used in energetic studies of starving zooplankton to a limited degree, because it does not reflect actual losses in organic matter and energy.

Losses in C, N, H, and individual J's followed an exponential pattern with a weak curvature. The maximum possible losses until death amounted to ca. 40 to 60% of initial values, depending on the parameter and larval stage under consideration. These observations correspond to those by Anger and Nair (1979) and Dawirs (unpubl. data) on starved larvae of *H. araneus* and *Carcinus maenas*, respectively. Ikeda (1974) reported reductions in biomass of other zooplankton down to 20%. Our figures also become higher if chitin is excluded from these calculations.

Anger and Dawirs (1981) found that feeding after initial starvation in Z-1 larvae of *H. araneus* is successful only if a certain time (point-of-no-return, PNR) is not exceeded. Comparing this time span with the above biomass data, the actual limits of starvation resistance are already reached when 25 to 30% of organic matter (C,N,H) or 30 to 35% of individual energy are lost. Beyond this PNR another ca. 10% loss in all these parameters is possible, before the larva dies, regardless of eventual food availability. Fifty percent of the larvae already reach this limit (PNR_{50}) when only ca. 20% of the organic substance or ca. 25% of energy is lost. The PNR values for the other stages have not yet been determined.

Another finding reported by Anger and Dawirs (1981) is that relatively short initial feeding periods suffice for zoeae of *H. araneus* to successfully reach the next stage (Z-2 or megalopa), regardless of further food availability. Converting these time spans to biomass data, a surprising agreement in both zoeal stages is found: 50% of the larvae reach this "point-of-reserve-saturation" (PRS_{50}), when they have gained ca. 70% N, 90% C and H each, and ca. 95% energy (related to early postmolt levels). If food is continually available, considerable further accumulation of organic matter and energy will take place (see above), but this additional reserve will not be needed before the next stage is reached. If no prey is available during this period (presumably premolt) the next stage will be significantly prolonged, thus revealing a certain dependence on reserves accumulated during the preceding zoeal stage. Anger and Dawirs (1981) suggested that sterols (precursors of the molting hormone, ecdysterone) may play a crucial role in this phenomenon.

It is doubtful that energetics alone can explain the early appearance of the PNR, since the actual losses in organic body substance are rather low at that time. We assume that an irreversible damage in some hormonal or enzymatic system is involved in ecdysis.

The weight-specific metabolic rate is a major factor deciding the maximal survival time under starvation (Ikeda 1974). It is far lower in starved as compared with fed zooplankton (see, e.g., Ikeda 1977 and earlier papers cited therein;

Mayzaud 1976; Logan and Epifanio 1978; Capuzzo and Lancaster 1979). The hyperbola-shaped decrease pattern in weight-specific energy (see above) is in accordance with that described by Mayzaud (1976) for respiration rates in starved zooplankton. There is an initial acclimation period with strongly decreasing metabolic rate, followed by more or less constant values. Our estimates for oxygen consumption follow this pattern, and their amounts compare favorably with literature data, if starvation and relatively low temperature (12°C) are taken into account (for review see Schatzlein and Costlow 1978).

In a low temperature range, high Q_{10} values are to be expected. This assumption is confirmed by extremely long survival times observed by Anger and Dawirs (1981). These figures of starvation resistance as well as our calculations of weight-specific respiration rates fit the quantitative relationship between these two parameters described by Ikeda (1974).

The metabolism of starved *H. araneus* larvae is mainly based on protein degradation (Anger and Nair 1979). According to the literature, this is a general feature in crustaceans (e.g., Mayzaud 1976; Ikeda 1977 and earlier papers; Capuzzo and Lancaster 1979). Our observations on changes in the C:N ratio suggest that during the final (premortal) period of long-term starvation, lipids also become important as a last reserve. However, at this time the larva is already doomed to die, regardless of eventual food availability, since the PNR has been exceeded (Anger and Dawirs 1981).

The amount of reserve and proportions of metabolic pathways apparently are also subject to annual and seasonal variation, possibly even to differences among different parts of one brood (e.g., Regnault 1969; Pandian and Schumann 1967; Pandian 1970; Pandian and Katre 1972; Anger and Dawirs 1981). Those changes may also explain differences between daily energy losses in starved zoeae estimated by Anger and Nair (1979) and in the present study. Future investigations will have to examine the amount and significance of such natural variation superimposed on the response patterns of decapod larvae in different feeding conditons.

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A MULTISPECIES ANALYSIS OF THE COMMERCIAL DEEP-SEA HANDLINE FISHERY IN HAWAII

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ABSTRACT

In the Hawaiian Islands 13 species of bottom fish are commonly harvested in the commercial deep-sea handline fishery. These are all high-level carnivores, including snappers, jacks, and a species of grouper, which are sought in water depths ranging from 60 to 350 m. Cluster analyses performed on the Hawaii Division of Fish and Game commercial catch report data suggest the existence of three bottom fish species groups which apparently segregate on the basis of depth distribution. These groups seem to be stable through time and similar among differing geographic localities.

Two measures of fishing effort, catch-records and fisherman-days, were compared to determine which is more suitable for use in stock-production analyses. Fisherman-days was selected because, among other reasons, it repeatedly demonstrates a stronger negative correlation with catch per unit effort.

Application of the Schaefer stock-production model to this multispecies fishery on a species-by-species basis provides an inadequate description of productivity. When catch statistics are aggregated according to the three cluster analysis species groups the results are much improved. In this regard consistently significant results and production estimates were obtained from the Maui-Lanai-Kahoolawe-Molokai bank, a region which presently accounts for about half of the total Hawaii catch. No significant interaction among the cluster groups was detected. When all 13 bottom fish species are analyzed together, the results are in agreement with the preceding analysis. Examining the aggregation process suggests that the model based on the intermediate level of aggregation (cluster groups) explains slightly more of the variation in total catch than does the model which treats all 13 species together.

We estimate the annual maximum sustainable yield of the commercial deep-sea handline fishery around the Maui-Lanai-Kahoolawe-Molokai bank to be 106 metric tons or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this maximum-sustainable-yield level.

Effective management programs for tropical fisheries are difficult to achieve (Pauly 1979). Often attempts at managing these fisheries are based on the application of inappropriate models to sparse data. Both deficiencies are due in part to the multiplicity of fish species inhabiting tropical environments. This great diversity (Sale 1977; Talbot et al. 1979) makes it difficult to compile adequate data for all species of interest. The Hawaiian Islands, which straddle the Tropic of Cancer, possess a relatively impoverished tropical ichthyofauna, yet between 600 and 700 species are known from this region (Gosline and Brock 1960). Coupled with high diversity, many tropical countries lack a refined statistical system for the acquisition and storage of fisheries data. In concert these two limitations impose severe restrictions on the quantity and quality of data which are currently available for the analysis and management of tropical fisheries (Pope 1979). Furthermore, classical fisheries models thus far developed have been directed toward the management of temperate and boreal stocks (Food and Agriculture Organization of the United Nations (FAO) 1978). These models usually treat species as independent management units. It has become apparent that such an approach is often inadequate when extrapolated to the tropics where community dynamics become increasingly important (Pauly 1979).

The multispecies approach to managing fisheries exploitation in complex ecosystems has only recently acquired a substantive base in the literature. Early work by Larkin (1963, 1966)

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evaluated the consequences of Lotka-Volterra competition and predator-prey systems on optimum exploitation strategies. Paulik et al. (1967) examined the problem of maximizing the yield from a fishery composed of mixed stocks, each with a unique spawner-recruit curve. A large body of descriptive work has documented the successional nature of changing catch composition which is often characteristic of increasing exploitation in a multispecies fishery (e.g., Regier 1973). Several recent multispecies investigations present highly sophisticated ecosystem models that require numerical solution and/or dynamic simulation, as well as numerous parameter estimates (Parrish 1975; Andersen and Ursin 1977; Laevastu and Favorite 1978[3]).

An alternative to this latter approach simply treats multispecies fisheries as though they behave as would a single species stock and evaluates production by application of the total biomass Schaefer model (TBSM) (Pope 1979). Brown et al. (1976) estimated total finfish production in the northwest Atlantic in this manner, as did Brander (1977) for demersal fish and shellfish in the Irish Sea. A review of this approach shows that "these overall Schaefer models generally seem to fit the data rather better than the fits experienced with their component stocks" (FAO 1978). Among the possible reasons for this are 1) the TBSM really presents a more realistic representation of multispecies fisheries than does summing the yields of individual stocks, 2) the better fit results from some type of averaging process, 3) artifacts in the method of fitting and/or shifts in preference between species within a fishery may result in a better fit when total biomass is evaluated (FAO 1978; Pauly 1979; Pope 1979). Several authors have issued the caveat that a thorough understanding of trophic relations is fundamental to managing any multispecies fishery and that such considerations may easily invalidate the application of the TBSM (May et al. 1979; Pauly 1979).

This paper estimates the productivity of deep-dwelling bottom fish stocks around the main islands of the Hawaiian Archipelago using stock-production methods. The fishery for these stocks is conducted in offshore waters ranging in depth from 60 to 350 m where a variety of species, principally snappers of the Family Lutjanidae, abound. In addition to providing preliminary productivity estimates for this fishery, an examination of the performance of the TBSM at various levels of species aggregation is undertaken. This latter analysis provides a quasi-quantitative means of evaluating the applicability of the TBSM to the Hawaiian offshore handline fishery.

SOURCES OF DATA AND DESCRIPTION OF THE FISHERY

In the State of Hawaii, all fishermen who sell a portion of their catch must be licensed as commercial fishermen by the Hawaii Division of Fish and Game (HDFG). There is no licensing requirement for recreational fishing. New commercial licenses are issued every fiscal year and once licensed, fishermen are required to submit a monthly catch report whether or not they have fished. These monthly catch reports require from each fisherman entries on the days and areas in which he fished, the types of fishing gear used, the number of individuals and pounds of the different species landed, and the dollar value of the catch. Incomplete reporting is thought to be common and raises the question of bias in the data (Ralston 1979[4]). Perhaps more serious is the omission of any direct measure of fishing effort or fishing power in the information concerning bottom fish obtained from these reports.

Monthly catch reports are coded, keypunched, and stored on magnetic tape for future use by HDFG. These data are the basis of this study and currently span the 20-yr period 1959 to 1978 inclusive, comprising some 600,000 records. While the date are voluminous, the extent of nonreporting by recreational fishermen and of incomplete or underreporting by commercial fishermen is unknown.

The complete HDFG data account for all types of commercial fishing in the State of Hawaii; therefore, only those catch records which list deep-sea handline fishing gear were used in this study. This reduced the data to one-fourth its original size and defined the scope of the fishery. Although the name suggests otherwise, the fishing gear is primarily hydraulic or electric

[3]Laevastu, T., and F. Favorite. 1978. Numerical evaluation of marine ecosystems. Part 1. Deterministic bulk biomass model (BBM). NWAFC Process. Rep., Natl. Mar. Fish. Serv., NOAA, Seattle, Wash., 22 p. (Unpubl. rep.)

[4]Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. (Unpubl. rep.)

although some manual equipment remains in use.

The fishery mainly exploits 13 categories of fish species (Table 1). Confusion concerning the taxonomy of species in the family Carangidae prohibits a more detailed classification of these forms although *Pseudocaranx dentex* and *Caranx ignobilis* probably account for the majority of ulua landed in Hawaii. While *P. dentex* is abundant in the Northwestern Hawaiian Islands, it is apparently uncommon around the main high islands (Uchida[5]). Further confusion is apt to result from the findings of Anderson (1981), who recently revised the genus *Etelis* and changed the names of both Hawaiian species. In addition, two hogfish species are frequently taken, *Bodianus bilunulatus* and *B. rulpinus*, although the former species seems to inhabit somewhat shallower depths than the latter. Of those species listed, most are caught almost exclusively with deep-sea handline gear. The exceptions are ta'ape, ulua, and a'awa which are commonly taken by several other methods (e.g., inshore handline, purse seine, gill net, etc.) (Ralston footnote 4). Catches of these species reported here include only those portions taken in the offshore handline fishery.

In descending order the dominant species in the fishery by weight are the opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala (Ralston footnote 4). These species taken together accounted for 86% of the total catch by weight in 1978, nearly all of which was marketed in Hawaii as fresh fish. Total landings from the fishery have remained relatively constant from 1959 to 1978, showing a slight increase in recent years, although higher catches were briefly reported during the late 1940's and early 1950's (Fig. 1) (Ralston footnote 4). Most of these species are highly prized and in recent years have averaged close to $5.00/kg ex-vessel.

In the past about 85% of the catch of deep dwelling bottom fish has been made around the main Hawaiian Islands in contrast to the uninhabited Northwestern Hawaiian Islands (Grigg and Pfund 1980). Catches from the latter area have increased remarkably in the last 2 yr, as larger, more seaworthy vessels have entered the fishery. Nonetheless, the lack of sufficient data

TABLE 1.—Principal species of fish landed in the Hawaiian offshore handline fishery.

Family	Species	Common name	Average weight (kg)
Lutjanidae	*Aphareus rutilans*	Lehi	3-8
	Aprion virescens	Uku	2-8
	Etelis coruscans	Onaga	2-8
	E. carbunculus	Ehu	0.5-2
	Lutjanus kasmira	Ta'ape	0.5
	Pristipomoides filamentosus	Opakapaka	1-6
	P. sieboldii	Kalekale	0.5
	P. zonatus	Gindai	0.5-2
Carangidae	*Caranx* and *Carangoides* spp.	Ulua	1-10
	Seriola dumerili	Kahala	3-10
Serranidae	*Epinephelus quernus*	Hapu'upu'u	3-10
Labridae	*Bodianus* spp.	A'awa	1-3
Scorpaenidae	*Pontinus macrocephala*	Nohu	1-2

[5]R. N. Uchida, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, pers. commun. November 1980.

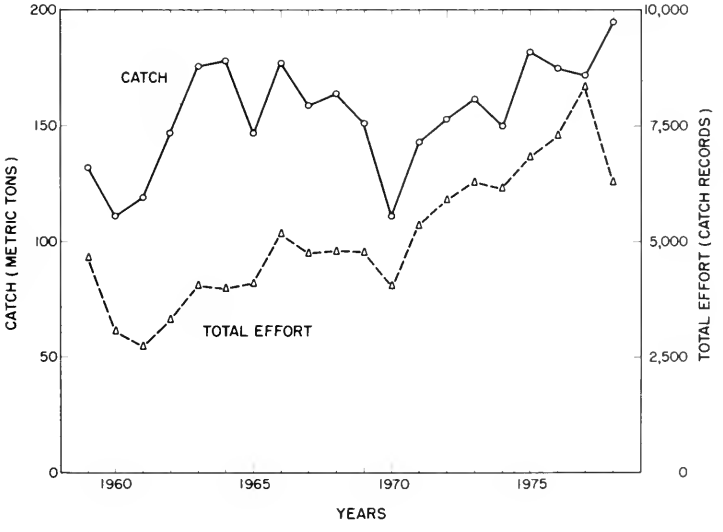

FIGURE 1.—Annual landings and total annual effort for the commercial deep-sea handline fishery in the main high islands of the Hawaiian Archipelago.

from this region prevents its analysis; the results presented here pertain only to the eight main islands of the archipelago (Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau, including Kaula Rock). Within this region fishing is conducted on offshore banks and pinnacles, primarily in the vicinity of the 100-fathom isobath. In the Hawaiian Islands the sea bottom typically extends away from shore at a depth of 30 fathoms for some distance and then falls abruptly to very great depths over a relatively short horizontal span (Brock and Chamberlain 1968). Most fishing occurs in this steep dropoff zone. Hence it is possible to crudely estimate the relative amount of total bottom fish habitat around a fishing bank by determining the length of the 100-fathom isobath surrounding it (Table 2). The maximum depth between the islands of Maui, Lanai, Kahoolawe, and Molokai (MLKM) is <100 fathoms; therefore, they were pooled and treated as a single bank (Fig. 2). All bottom fish taken from a bank were considered one stock because movements of juveniles and adults across deep water from one bank to the next are highly improbable whereas lateral movements around the perimeter of the 100-fathom isobath of a bank cannot be discounted. The Islands of Oahu and Hawaii are separated by deep water from all other islands and banks, hence, by definition, they harbor distinct stocks. Kauai, Niihau, and Kaula Rock (KNK), although separated across short distances by deep water, were analyzed together because they present a similar fishing profile and they are closely situated to one another. Thus, based on this classification four distinct stocks were analyzed independently. The extent of larval dispersal between these stocks is unknown at present but is currently under study (Shaklee[6]). A more detailed description of this fishery may be found in Ralston (footnote 4) or in Hawaii Department of Land and Natural Resources (1979).

TABLE 2.—A list of the four banks which harbor separately defined stocks. The length of the 100-fathom isobath around a bank roughly measures the extent of its bottom fish habitat.

Bank	Percent contribution to total landings	Approximate length of 100-fathom isobath (nmi)
Hawaii	21	290
MLKM[1]	56	390
Oahu	12	150
KNK[2]	11	195

[1]Maui-Lanai-Kahoolawe-Molokai.
[2]Kauai, Niihau, and Kaula Rock.

FISHING EFFORT

The ultimate goal of any stock-production analysis is to relate the impact of variable fishing pressure on stock abundance. Fishing pressure

[6]J. G. Shaklee, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, HI 96744, pers. commun. 1979.

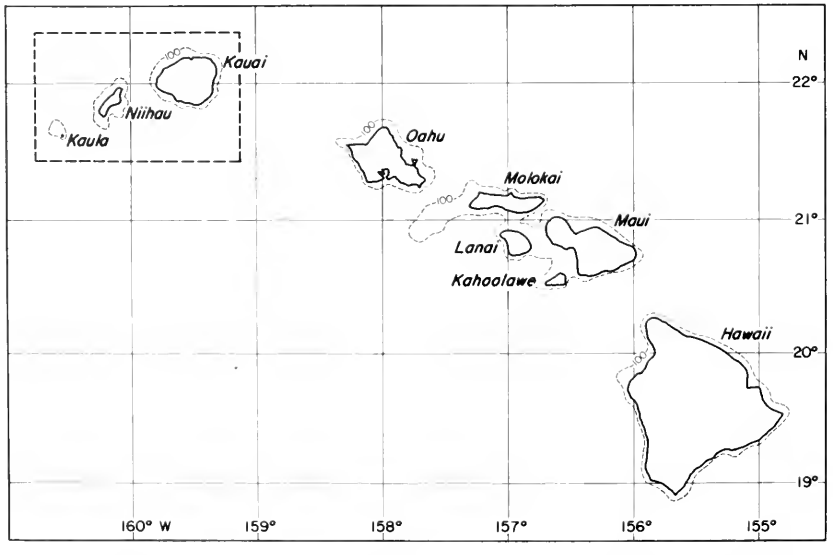

FIGURE 2.—Map of the eight main Hawaiian Islands and Kaula Rock with the 100-fathom isobath included.

is most conveniently formulated as instantaneous fishing mortality (F), measured over some arbitrary interval of time, usually 1 yr (Ricker 1975). Frequently it is not possible to measure F directly, however, and so a proportionate measure of F is selected, i.e., fishing effort or f. The ideal choice of units for fishing effort results in a linear correspondence between F and f, a zero intercept, and minimal residual variance (Rothschild 1977). Because F is frequently unknown, it is often difficult to ascertain whether these criteria are met and yet the selection of an appropriate measure of fishing effort is most critical to meeting the assumptions of a stock-production analysis. Ample consideration should be given to these factors before the data are collected.

No attempt has been made in the HDFG data to record either the fishing effort or the fishing power of individual fishermen. A suitable measure of fishing mortality in this fishery would be the cumulative number of hook-hours or line-hours of fishing. While such figures are currently unavailable, it has been possible to determine the total number of fishing records filed in a year which report the catch of a particular species. This statistic, the number of daily reports by fishermen who have caught any one particular species, was frequently computed and is termed catch-records. Figure 1 presents, in addition to the catch, the total number of deep-sea handline catch-records filed from 1959 to 1978 concerning all 13 species of bottom fish. This measure of fishing effort does not always correspond to the number of fisherman-days because one operator may catch several species during a single day of fishing. In this instance the reporting of each particular species comprises one catch-record. Thus, when aggregated species groups are considered, the number of fisherman-days will always be fewer than the total number of catch-records. When species are considered independently of one another the two figures are equal (catch-records = fisherman-days).

Interpreting the meaning of a fisherman-day as a unit of fishing effort in this fishery is difficult. It was tabulated by following the daily reports of individual fishermen, identified by their commercial fishing license numbers. All commercial fishermen in Hawaii, whether captain or crew, must have a license. It is likely that many catch reports are filed only by boat captains who document the landings of an entire fishing vessel, which may have a variable number of crew members. Thus a fisherman-day, as defined here, may reasonably be thought of as a vessel-day. However, because this unit of effort is defined and specified on the basis of commercial fishing licenses, in the interests of exactitude, we have chosen to use the term fisherman-day.

RESULTS

Clustering

The usual method of aggregating catch data would be to pool all 13 deep-sea handline species into a single group and to analyze the total with the TBSM. An alternative is to employ a multivariate statistical procedure to assess the degree of colinearity among species and to define species groups based on the strength of interspecies associations in the catch (Pope 1979). Such an approach would identify those bottom fish which tended to appear with one another in the catch to the exclusion of others and would measure the extent of correlation of fishing mortality among species. Pope (1979) has termed this "technological interaction" and has discussed its importance in multispecies fisheries. Separate application of the TBSM to each species group formed by clustering would constitute an analysis performed at an intermediate level of species aggregation. Conceptually this is desirable because in the Hawaiian offshore handline fishery different species are known to exhibit stratification by depth (Strasburg et al. 1968).

Cluster analyses were performed with a computer routine (Dixon 1977, program P1M) where the 13 species of bottom fish comprised the variables to be clustered and the catch from a single day's fishing formed one case. Associations were computed on the basis of the landed weight of each species. The average linkage between groups defined the criterion for amalgamating clusters and correlation coefficients were used as measures of similarity.

Separate analyses were performed for each of the four designated bank (Table 2) areas to assess whether obvious differences exist among banks with regard to interspecies associations. Similarly, separate analyses were conducted for the years 1959, 1965, 1971, and 1977 to see whether temporal variation in species grouping is an important factor to consider.

No striking differences or patterns emerged from these various comparisons. The intrinsic

variation apparent between clusters obtained from the same bank in 3 adjacent years (Hawaii in 1976, 1977, and 1978) was as great as the variation in clustering found between different banks and through longer periods of time. While there were a few suggestions of differences in the species composition of groups among the four banks, these were relatively minor and were ignored. Only one fairly consistent pattern of grouping was repeatedly exhibited across banks and through time, and this was confirmed by a single clustering of all the data pooled together. This pattern shows that the bottom fish fishery is loosely composed of three species groups which are apparently segregated on the basis of the depth range of member species (Table 3) (for depth distributions see Gosline and Brock 1960; Brock and Chamberlain 1968; Strasburg et al. 1968). These groups represent species assemblages which are for the most part independent of time and/or geographic location.

The delimitation of these three species groups is somewhat arbitrary and should not be viewed as the only way in which an intermediate level of species aggregation of the catch could be achieved. Nevertheless this grouping structure is reasonable and its use enhances the biological realism of the multispecies model by identifying and classifying those species which seem to share the greatest correlation in fishing mortalities. In addition the grouping structure allows an assessment of the effect aggregation has on the fit of data to a Schaefer stock-production analysis. A brief discussion of each of these groups is appropriate.

The appearance of ulua, ta'ape, and a'awa in the shallowest group (Group I) is consistent with the observation that these three species are frequently harvested with other types of fishing gear. Members of this group are often seen by scuba divers who venture below 30 m, although the vertical distribution of these species in the deep-sea handline fishery is centered around the 60 m terrace which circles much of the Hawaiian Islands (Brock and Chamberlain 1968). Because the name ulua refers to several different carangid species, one of which (*P. dentex*) is most often taken with members of Group II in deeper water, it is evident that some inaccuracies in the classification exist. This particular defect is not so much a result of the clustering process as it is a result of faulty data. Kahala, on the other hand, range widely (Gosline and Brock 1960) and are known from throughout the depth ranges of both Groups I and II and occur even shallower. Its position in Group II may simply reflect the relatively greater fishing pressure exerted in the 100-200 m depth range where other members of Group II, such as the opakapaka and hapu'upu'u, are centered. The deepest group (Group III) is particularly well defined and is composed of three lutjanid species, two of which are deepwater eteline red snappers.

TABLE 3.—Bottom fish species groupings defined by cluster analysis.

Group	Species	Approximate depth range (m)
I	Ulua, uku, ta'ape, a'awa	30-140
II	Opakapaka, hapu'upu'u, kahala, gindai, lehi, nohu	80-240
III	Onaga, ehu, kalekale	200-350

Fishing Effort

An attempt was made to evaluate the two measures of fishing effort, catch-records and fisherman-days, on the basis of their correlation with catch per unit of effort (CPUE). The Schaefer model predicts that plots of CPUE against effort should demonstrate a linear relationship with a negative slope if the production of the stock is described by the logistic growth curve (Ricker 1975). Such a prediction generates a one-tailed test of the hypothesis that $\rho \geq 0$ against the alternative hypothesis that $\rho < 0$ where ρ is the population correlation coefficient between CPUE and f. Even though a negative correlation between CPUE and effort is expected in a situation where catch and effort are completely unrelated random variables, the degree of spurious correlation due to this effect will be small if the main cause of variation in CPUE is varying stock abundance (Gulland 1974).

Correlations were computed between these two variables, using both measures of fishing effort for each species group-bank combination ($3 \times 4 = 12$). Additional correlations were computed for the total aggregated catch from each of the four banks ($1 \times 4 = 4$), resulting in 16 comparisons of the two measures of effort (Table 4). Comparisons which might be based on treating species as independent stocks are inappropriate here because the two measures of effort become equal in this limiting case. One means of evaluating the effectiveness of these two measures is to compare the signs of the correlation coefficients (r) and the magnitudes of the coefficients of determination (r^2) for each. It

TABLE 4.—Comparisons of correlations of CPUE and fishing effort (f) for two different measures of f. The total aggregate incorporates all 13 species.

		Unit of fishing effort			
		Catch-records		Fisherman-days	
Group	Bank[1]	r	r^2	r	r^2
I	Hawaii	−0.095	0.01	−0.128	0.02
	MLKM	−0.358	0.13	[2]−0.503	0.25
	Oahu	−0.153	0.02	−0.259	0.07
	KNK	−0.180	0.03	−0.111	0.01
II	Hawaii	−0.111	0.01	−0.120	0.01
	MLKM	−0.379	0.14	[2]−0.769	0.59
	Oahu	+0.285	0.08	+0.293	0.09
	KNK	+0.481	0.23	+0.237	0.06
III	Hawaii	−0.187	0.03	−0.015	0.00
	MLKM	−0.240	0.06	[2]−0.502	0.25
	Oahu	−0.362	0.13	[2]−0.390	0.15
	KNK	−0.308	0.09	[2]−0.395	0.16
	Total aggregate				
	Hawaii	−0.150	0.02	−0.334	0.11
	MLKM	[2]−0.463	0.21	[2]−0.878	0.77
	Oahu	[2]−0.465	0.22	[2]−0.521	0.27
	KNK	+0.395	0.16	−0.165	0.03

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK= Kauai, Niihau, and Kaula Rock.
[2]Significant at $P = 0.05$ level, one-tailed test, df = 18.

is apparent that in 13 of the 16 possible comparisons, fisherman-days showed a stronger negative correlation with CPUE than did catch-records. Based on these results we conclude that fisherman-days predicts the behavior of CPUE more precisely than catch-records. Use of this measure also eliminates repeated counting of effort statistics when more than one species in a group is caught on a particular day and has greater intuitive appeal as well. For these reasons we conclude that fisherman-days is the best measure of fishing effort available at present. It is worth noting that these two different measures of effort are approximately linear in their relationship to one another, implying that the superiority of fisherman-days over catch-records as a measure of effort is probably due to a smaller residual variance of instantaneous fishing mortality (F) on the former statistic than on the latter.

Stock Production Analyses

In this section the Schaefer model is applied to the deep-sea handline data in which the catch is aggregated at three different levels. At the first level a single-species Schaefer model is fitted to each species separately. Next, the TBSM is fitted to each of the three species groups delimited by the cluster analysis. In the final section the total aggregated catch of all 13 species taken together is analyzed with the TBSM. Fisherman-days was used as the measure of fishing effort throughout, but equilibrium approximation (Gulland 1972) was not attempted because no information was available concerning the longevity of these species and a previous application of this method to the data had shown little improvement in the results (Ralston footnote 4).

When each species is treated independently there are 52 separate analyses (4 banks with 13 species each). In only two of these regressions of CPUE on f is the null hypothesis $\beta \geq 0$, where β is the slope of the regression, rejected in favor of the alternative hypothesis $\beta < 0$. Both involved the MLKM bank where opakapaka ($t = -2.91$, df = 18) and uku ($t = -1.82$, df = 18) demonstrated significant inverse regressions in which respectively, 32% and 16% of the total variation in CPUE were explained. The significance of these two regressions can easily be attributed to the Type I error and consequently nothing can be concluded from these results concerning the productivity of these fishes.

The fit of the TBSM to the data is much improved when the three species groups are considered. The model was applied to the HDFG data 12 times; once for each species group and bank combination. Significant results ($P = 0.05$, one-tailed test) were obtained in 5 of the 12 applications of the model (Table 5). The three analyses from the MLKM bank were significant in every case and those for Group III were significant in three out of the four regressions tested. The observation that the results from the remaining banks and species groups are not significant is not so disturbing because 56% of all bottom fish landings are harvested from the MLKM bank (Table 2). An estimate of the maximum sustainable yield (MSY) and optimum effort was then computed for each of the five significant combinations, as well as a standardized measure of productivity, calculated as the sustainable yield of bottom fish per nautical mile of 100-fathom isobath. Assuming logistic growth of the stocks the catchability coefficient was estimated using the computer program PRODFIT (Fox 1975). The t value in the table refers to the test of the null hypothesis that the slope of a regression is zero or positive.

Pope (1979) has proposed an interactive model to describe multispecies fisheries in which total yield is depicted as the sum of the yields of individual species with additional terms to account for community interactions. In the simple two-species case the equation describing surplus production (Y) is:

TABLE 5.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where species have been aggregated according to cluster analysis species groupings.

Bank[1]	Species group	MSY[2] (kg/yr)	Optimum effort (fisherman-days)	MSY/nmi 100-fathom isobath	Catchability coefficient	t value (df = 18)
MLKM	I	23,000	480	60	0.00180	−2.47
	II	48,800	662	125	0.00062	−5.11
	III	31,900	396	82	0.00120	−2.46
Oahu	III	1,900	119	12	0.00280	−1.74
KNK	III	4,800	84	25	0.00600	−1.77

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai
KNK = Kauai, Niihau, and Kaula Rock.
[2]MSY = maximum sustainable yield.

$$Y = a_1N_1 + a_2N_2 - b_1N_1^2 - b_2N_2^2 + (c_1 + c_2)N_1N_2 \quad (1)$$

where N_1 and N_2 refer to the population sizes of species one and two and a_1, a_2, b_1, b_2, c_1, and c_2 are model parameters (Pope 1979). This model is the sum of two single-species surplus production models with the additional term $(c_1 + c_2)N_1N_2$ to account for the interaction between the two species. Depending upon the signs of c_1 and c_2 the equation models predation, competition, or mutualism. More importantly, the sum of these two parameters determines the impact of the interaction on the sustainable yield of the system.

The question of whether significant interaction occurs among the cluster-analysis species groups was examined by considering the MLKM bank alone. The regressions of all three cluster groups were highly significant from this region and further treatment of these data is therefore considered appropriate.

In the three-species version of Equation (1) there are three terms involving the sum of c parameters. In this analysis a species group (I, II, or III) is treated as though it were a single species and the a and b parameters necessary to evaluate the equation were taken from the independently calculated regressions of Table 5. A nonlinear regression routine (SAS Institute 1979, program NLIN) was employed to estimate the sums of the various c parameters for the MLKM bank (Table 6). It is apparent that these sums do not differ significantly from zero and hence there is no evidence for significant interaction among groups. This result further supports the classification of species into independent assemblages for use in an aggregated treatment of the data.

In the final analysis all species were treated as a single group and the TBSM was applied to the total aggregate. Of the four possible regressions of CPUE on f, both the MLKM and Oahu banks yielded significant results (Table 7). Similar computations were performed for these sites as had been done previously. In addition the regression of total bottom fish CPUE on f for the MLKM bank and the corresponding catch curve (catch versus effort) were plotted (Fig. 3). It is reassuring to note that the sum of the three-species group MSY's from this bank, calculated from the preceding analysis, amounts to 103,700 kg/yr. This estimate compares favorably with the present result (a difference of about 2%) though the two figures were computed somewhat independently. A comparison of MSY/nmi 100-fathom isobath between these two banks reveals the Oahu value to be substantially less than the MLKM value. Although this may in actuality represent differences in habitat quality and productivity between these banks, there is the possibility that the difference is at least partially due to a difference in the extent of unreported recreational fishing pressure between the banks.

The results of the stock-production analysis for the MLKM bank provide statistically acceptable regressions, yet the estimates of production are

TABLE 6.—Tests of whether interaction between cluster analysis species groups have a significant effect on total bottom fish yield from the Maui-Lanai-Kahoolawe-Molokai bank.

Term	Parameters	Evaluated value	95% confidence limits
$(c_1 + c_2)\ N_1N_2$	$(c_1 + c_2)$	0.242	(−0.244, 0.728)
$(c_2 + c_3)\ N_2N_3$	$(c_2 + c_3)$	0.185	(−0.284, 0.654)
$(c_1 + c_3)\ N_1N_3$	$(c_1 + c_3)$	−0.868	(−2.365, 0.629)

TABLE 7.—Significant applications of the total biomass Schaefer model to the Hawaii Division of Fish and Game data set where all species have been grouped into one total aggregate.

	Bank	
	MLKM[1]	Oahu
MSY[2] (kg/yr)	106,000	15,700
Optimum effort (fisherman-days)	901	424
MSY/nmi, 100-fathom isobath	272	105
Catchability coefficient	0.00080	0.00168
t value (df = 18)	−7.77	−2.59

[1]MLKM = Maui-Lanai-Kahoolawe-Molokai.
[2]MSY = maximum sustainable yield.

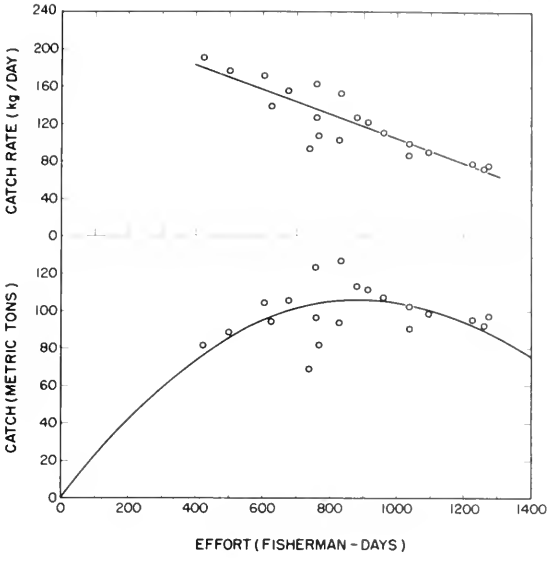

FIGURE 3.—Fitted production curves of CPUE and catch on fishing effort for the total aggregate landings of commercial bottom fish species from the Maui-Lanai-Kahoolawe-Molokai bank.

probably low. The HDFG data provide information on only a portion of the harvest of these species. Recreational bottom fishing is very popular around the main islands of the Hawaiian Archipelago but its relative impact is completely unknown. Furthermore, underreporting by commercial fishermen is also likely but its extent is hard to determine. Based on these considerations, the overall estimate of annual production calculated for the MLKM bank (272 kg bottom fish/nmi 100-fathom isobath) is best considered a lower bound for the surplus production obtainable from this type of fishery. In spite of the difficulty in determining precise estimates of productivity it would appear that the added effects of commercial and recreational fishing are close to fully exploiting the fishery (Fig. 3). In 1978 over 96 t (metric tons) of bottom fish were harvested from the MLKM bank by commercial fishermen.

DISCUSSION

Fishing Effort

One of the primary goals of this study has been to estimate the commercial productivity of Hawaii's offshore bottom fish resources. We have met with mixed success in our attempt because only one of the four study banks (Fig. 2) consistently provided significant results. In spite of this difficulty the MLKM is the largest of the four, producing well over half the total catch of bottom fish. The lack of statistical significance from the remaining banks may be due to several factors.

The impact of fishing is measured by correlating changes in fishing effort with catch rate (CPUE). If the observed range of fishing effort is too small to render an appreciable change in stock density then the impact of fishing cannot be measured. This hypothesis of insufficient variation in fishing mortality does not explain the lack of correlation between CPUE and effort from the Hawaii, Oahu, and KNK banks, however. The range in fishing intensity (defined as fisherman-days/nmi 100-fathom isobath or fishing effort per unit area) between the period 1959 and 1978 was the least for the MLKM bank where only a threefold difference in intensity was experienced. In contrast, fishing intensities ranged upwards from 4-fold (KNK) to 26-fold (Oahu) among the remaining banks. The range of fishing intensity to which the MLKM bank has been exposed is the least of all four sites and from this observation it would be reasonable to assume that all banks have experienced substantial variation in fishing mortality.

This follows logically only if the catchability coefficients for all banks are similar. It is probable, however, that these four regions differ with respect to the impact of one unit of fishing effort on the various stocks. If differences in fishable area are corrected for, a fisherman-day recorded from Oahu may well represent less fishing mortality than the same figure from the MLKM bank. In this regard, preliminary analyses based on fishing intensity rather than fishing effort showed that significant differences exist among the four banks in the relationship of CPUE to fishing intensity, precluding the option of pooling the data across banks (see Munro 1978 for a production analysis based on fishing intensity). In principle then, differences in catchability could explain the poor results from Hawaii, Oahu, and KNK if the catchability coefficient equating fisherman-days to fishing mortality from these areas is substantially less than that for MLKM. Variation in the extent of unreported catch among banks could compound this effect.

Other factors which remain unaccounted for

could further confound the interpretation of effort statistics. It is unknown whether the percentage of reported catch to total catch, among both commercial and recreational fishermen, is increasing, decreasing, or remaining stable. There has also been a trend toward increased fishing power with the advent of mechanical line haulers, but the exact amount of this effect is unknown. Considerations such as these make it difficult to quantify bottom fish effort statistics.

This brief discussion underscores the importance of employing an appropriate measure of fishing effort in which catchability does not vary according to the activities of man. It was possible to demonstrate the superiority of fisherman-days over catch records and yet the former measure proved to be inadequate when pooling across banks was attempted.

Effects of Aggregation

Investigators have reported that in a multispecies fishery the TBSM when applied to aggregated data often fits better than the Schaefer model applied on a species-by-species basis (FAO 1978; Pauly 1979; Pope 1979). We will examine this phenomenon for data from the MLKM bank for two levels of aggregation.

As shown in the results section we have applied the Schaefer model to CPUE and effort data at three levels of data aggregation. First we applied the Schaefer model to the data on a species-by-species basis. Then species were partitioned into three cluster groups, the catch and effort data were computed for each group, and the TBSM was fitted to each group. Finally all species were pooled into one group and the aggregate data consisting of total catch and effort were computed and fitted with the TBSM.

The fit of the TBSM to each of the three species groups and to the total group resulted in significant regressions for the MLKM bank while only 2 out of 13 single-species regressions for this bank were significant. This result may be due to the fact that the fishery exploits groups of species simultaneously and that our measure of fishing effort measures exploitation on species groups rather than single species. It is apparent that when the data in this study were progressively pooled, the correlation coefficients describing the fit became increasingly negative (Fig. 4). This result alone would suggest that aggregation led to a better fit. Unfortunately be-

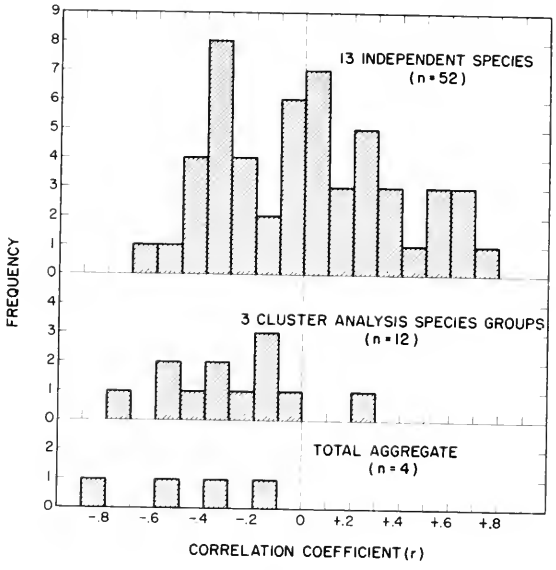

FIGURE 4.—Frequency distributions of correlation of coefficients between CPUE and fishing effort based on three levels of species aggregation.

cause only 2 out of the 13 single-species regressions were signficant, it is not appropriate to use the single-species results in our comparison of the effects of aggregation. Table 4 presents the correlation coefficients between CPUE and effort for each of the three cluster groups and the total aggregate. At first glance it appears that for the MLKM bank the TBSM applied to the total group fits substantially better ($r^2 = 0.77$ for fisherman-days) than the TBSM applied to any of the three species groups ($r^2 = 0.25$, $r^2 = 0.59$, and $r^2 = 0.25$). However, an examination of the correlations between fishing effort for the three cluster groups reveals that these variables are highly correlated (Table 8). Grunfeld and Griliches (1960) have cogently argued that increased colinearity of independent variables can lead to an increase in the goodness of fit (r^2) when data have been aggregated. This deceptive gain in the explanatory power of an aggregated independent variable prevents a direct compari-

TABLE 8.—Correlations of fishing effort (fisherman-days) (f) among cluster analysis species groups.

Group effort	$f1$	$f2$	$f3$
$f1$	1.000	0.943**	0.900**
$f2$	—	1.000	0.940**
$f3$	—	—	1.000

**Significant $P = 0.01$, df = 78.

son of the coefficients of determination obtained from different levels of grouping. Thus it is improper to compare the goodness of fit for the grouped analysis to that for the total aggregate without correcting for this bias. They suggest that a more appropriate and direct way of comparing the effect of these two levels is to compare the proportion of variance in the total catch explained by the predicted total catch from the two levels of aggregation. We must use catch rather than CPUE as the dependent variable because the sum of the CPUE values predicted from each of the grouped models will not predict total CPUE.

When annual catch (C) rather than CPUE is used the Schaefer model becomes

$$C = af - bf^2 + E \tag{2}$$

where a and b are constants, f is fishing effort in fisherman-days, and E is a normal random variable with mean 0 and finite variance. In the case when catch and effort are aggregated into the three species groups there will be three equations of the form of Equation (2) based on the grouped annual catch (C_i) and grouped annual effort (f_i) for $i = 1, 2, 3$. For the completely aggregated TBSM there will be a single equation of the form of Equation (2) with total annual catch (TC) and total annual effort (Tf). In all four equations the nonlinear regression coefficients a and b can be estimated with the 20 yr of annual data from 1959 to 1978. We can then use these coefficients to obtain predicted group annual catches ($\hat{C}_{ij}$) for groups $i = 1, 2, 3$ and years $j = 1, 2, ..., 20$, and the predicted total annual catches (TC_j) for years $j = 1, 2, ..., 20$ given the corresponding effort statistics.

We now have two estimates of total annual catch based on either TC_j from the fully aggregated TBSM or $\hat{C}_{1j} + \hat{C}_{2j} + \hat{C}_{3j}$ from the three species groups regressions. We can compare these two levels of aggregation based on their accuracy in predicting TC. This is done by defining SS_g to be the sum of squares of $TC_j - \hat{C}_{1j} - \hat{C}_{2j} - \hat{C}_{3j}$ for $j = 1, 2, ..., 20$, or the deviations of the grouped predicted catch from the observed total, and defining $s_g^2 = SS_g/19$. Let SS_t be the sum of squares of $TC_j - TC_j$, $j = 1, 2, ..., 20$, or the deviations of the predicted total catch of the completely aggregated TBSM from the observed total catch. Finally let $s_t^2 = SS_t/19$ and s_{TC}^2 be the sample variance of the total annual catch. Then the proportion of the variance of the total annual catch explained by the sum of the three species groups model is r_g^2 defined as:

$$r_g^2 = 1 - s_g^2/s_{TC}^2 \tag{3}$$

and the proportion of the variance in the total annual catch explained by the TBSM is r_t^2 defined as:

$$r_t^2 = 1 - s_t^2/s_{TC}^2 . \tag{4}$$

For the MLKM bank we determine $r_t^2 = 0.14$ and $r_g^2 = 0.18$. Thus the increased level of data aggregation going from treating the fishery as three separate groups to one total group does not in fact improve the fit of the catch curve although this appeared to be the case when the r^2 for the TBSM applied to the total group was compared to the r^2 values for the TBSM applied to each of the three cluster groups (Table 4, Fig. 4). As outlined previously these coefficients of determination, as calculated above, refer to the prediction of catch from effort data, for which the fit is substantially poorer than the fit of CPUE on effort.

A consideration of statistical aggregation theory has shown that the classification of bottom fish species into cluster groups results in slightly better predictions of total bottom fish catch than does analysis of the total aggregate. Since superior performance is achieved at an intermediate level of aggregation, it is possible to discount the undesirable effects of "averaging" which have troubled previous investigators (FAO 1978; Pauly 1979; Pope 1979). Furthermore, the lack of significant interaction among the species groups (Table 6) suggests that this particular application of the TBSM to the Hawaiian offshore handline fishery is appropriate.

Even though the separation of data from the MLKM bank into three species groups produced only a marginally better fit than the total aggregate model and the extra computations which are necessary were extensive (e.g., clustering), some advantage can be gained by splitting the fishery up into the groups listed in Table 3. Not only is the biological realism of the stock-production analysis enhanced but interesting patterns are also allowed to emerge. Notice, for example, that while the estimate of MSY for Group I from the MLKM bank is less than that for Group III from the same bank (Table 5), the fishing effort required to reach that figure is

substantially greater, in spite of the fact that the catchability coefficient for Group I is greater than for Group III. This apparent contradiction can be understood when estimates of carrying capacity and instantaneous growth rate are computed for the two groups. Ricker (1975) showed that the virgin shock biomass (B_∞) is equal to a/q and the intrinsic rate of natural increase (r) is equal to aq/b, where q is the catchability coefficient and a and b are the intercept and slope, respectively, of the regression of CPUE on effort. Using these equations the estimate of virgin biomass for Group I at the bank is much less than for Group III whereas the intrinsic rate of natural increase for Group I is nearly double that of Group III, hence, the disparity in catchability coefficients. This manner of evaluating the growth dynamics of the fishery implies that if fishing were to stop abruptly, Group I would recover to pristine levels much sooner than either Group II or III. Thus, this analysis would predict that a form of succession would occur around the MLKM bank if fishing were curtailed as a new equilibrium point was approached. Although there is little hope of manipulating the system to test this particular prediction of the model, this type of heuristic calculation can provide valuable insights concerning the consequences of different management programs.

Pope (1979) has shown that in a multispecies fishery an increase in the colinearity of effort values among species or groups will result in a more parabolic-shaped yield curve. Consequently, he argues that if fishing pressure is exerted in such a way that the fishing mortalities of the various species remain in constant ratio to one another, then the use of the TBSM is a realistic management option. He points out though, that it cannot be concluded that an MSY estimated by application of the model to actual data is anywhere near the global maximum of the system. These considerations bear directly on this study because of the high correlations of fishing effort among the three species groups. Even though MSY from the MLKM bank is estimated to be 106 t/yr it is quite possible that a substantially larger yield could be sustained if it were possible to alter the ratios of fishing mortality among the species groups. This possibility is not unrealistic because these groups seem to be for the most part spatially separated. In principle then, appropriate management action could reduce fishing effort on one group while simultaneously increasing that on another, but at present it is impossible to speculate about what the global MSY of the MLKM bank might be.

One of the least realistic aspects of the TBSM is its inability to adequately model trophic dynamics (Pauly 1979). The addition of Lotka-Volterra interaction terms to the model (Pope 1979) is a relatively simplistic attempt to deal with this problem. Pauly (1979) argued that the surplus-yield of fish predator-prey systems may be overestimated by the TBSM because of "prudent predation" by top carnivores. This theory (Slobodkin 1961) would propose that fish predators optimally harvest their fish prey, leaving little or no remaining latent productivity of the prey species for man to utilize. These arguments must impose group selectionist reasoning and suffer as a result. Nevertheless, the TBSM assumes that total stock size is greatest in a virgin state, a condition which need not be satisfied if limitation is internally imposed (May et al. 1979).

Fortunately these considerations do not detract from the value of the present analysis. The six dominant species in the fishery (opakapaka, ulua, uku, onaga, hapu'upu'u, and kahala) are all high-level carnivores and occupy a similar trophic position. No predator-prey relationship is known to exist between any of the 13 species listed in Table 1, although extensive gut content analyses of all life history stages are currently unavailable. Thus, some of the objectionable aspects of the TBSM have been minimized by not including species from different trophic levels within the same analysis. Predator-prey relationships in a fisheries context are poorly understood at present and will probably require a more dynamic construct than the TBSM is capable of offering (May et al. 1979; Pauly 1979).

SUMMARY

Examining the HDFG catch report data shows that the commercial deep-sea handline fishery in the Hawaiian Islands is a multispecies fishery composed principally of 13 species of bottom fish, 6 of which comprise 86% of total landings. Snappers (Lutjanidae), jacks (Carangidae), and a species of grouper (Serranidae) dominate the catch, all of which are high-level carnivores.

In the main high islands of the Hawaiian Archipelago (see Figure 2) three bottom fish

species groups are recognized based on cluster analyses which measure the tendencies of the various species to appear with one another in the catch. These groups seem to segregate on the basis of depth distribution, providing convenient biological assemblages for aggregating catch statistics.

Application of the Schaefer stock-production model to this fishery on a species-by-species basis provides an inadequate description of productivity. When species are aggregated into the cluster groups and analyzed with TBSM, the results are much improved. In this regard consistently significant results and production estimates were obtained from the MLKM bank, a region which presently accounts for half of the State of Hawaii's catch. No significant interaction among these groups was detected. When all 13 species are analyzed together, the results are in agreement with the preceding analysis. Based on TBSM applied to the MLKM bank, we estimate the annual MSY of the commercial deep-sea handline fishery to be 106 t or about 272 kg/nmi of 100-fathom isobath. Because recreational catch is unaccounted for, these figures are considered lower bounds for the gross production obtainable from this type of fishery although currently the commercial fishery is operating close to this MSY level.

By examining the effect of aggregating catch statistics we show that the production models based on the intermediate level of catch aggregation (cluster groups) together explain slightly more of the variation in the total catch than does the production model based on the total aggregate catch in spite of a higher coefficient of determination resulting from the latter analysis. High correlations of fishing effort among cluster groups account for this nonintuitive result.

Application of the Schaefer stock-production model to catch and effort data aggregated over species can be a useful tool for the analysis of a multispecies fishery. The appropriate level of aggregation will depend on biological and geographic factors.

ACKNOWLEDGMENTS

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DEVELOPMENT AND APPLICATION OF AN OBJECTIVE METHOD FOR CLASSIFYING LONG-FINNED SQUID, *LOLIGO PEALEI*, INTO SEXUAL MATURITY STAGES

WILLIAM K. MACY III[1]

ABSTRACT

An objective method of classifying long-finned squid, *Loligo pealei*, by their sexual maturity was developed using cluster and discriminant analysis techniques. The resulting system recognizes four developmental stages and employs a maximum of only five easily measured morphometric parameters. Such a system is easy to use and is suitable for large-scale field studies with relatively untrained help. The value of determining clearly recognized reproductive stages is demonstrated by an application of the method.

Each summer schools of long-finned squid, *Loligo pealei* Lesueur, 1821, move into shallow coastal waters from Delaware Bay to Cape Cod to spawn (Verrill 1882; Haefner 1964; Summers 1968, 1971). During the colder months, however, the squid are found only offshore, concentrated in canyon mouths along the continental slope (Summers 1967, 1969; Vovk and Nigmatullin 1972; Serchuk and Rathjen 1974). While the size/age composition of the species has been relatively well described by Verrill (1882), Summers (1967, 1968, 1969, 1971), Tibbetts (1975, 1977), and Mesnil (1977), many details of its reproductive cycle, particularly during the offshore period, remain unclear (see Summers 1969, 1971; Vovk 1972; Arnold and Williams-Arnold 1977; Mesnil 1977). From such studies it appears that *L. pealei* lives only 12-18 mo on average, and that like most squid it dies after spawning (Arnold and Williams-Arnold 1977). Details of the reproductive biology and population structure of such a short-lived species, with only two year classes at most, are especially important in the development of prudent stock management programs. Unfortunately, no single method for characterizing the reproductive state of individuals of this species has been employed to date.

A number of classification methods have been employed for a variety of squid species, which reflect both interspecific differences and differing requirements of the investigators using them (Tinbergen and Verwey 1945; Mangold-Wirz 1963; Fields 1965; Hayashi 1970; Vovk 1972; Holme 1974; Ikehara et al. 1977; Durward et al. 1978; Juanicó 1979; Hixon 1980). Many of these methods are slow because of the large number of variables required or the need for sample weighing or microscopic examination. Some methods also rely mainly on subjective distinctions.

From 1975 through 1978, ecological studies concerning the population structure, movement patterns, and feeding habits of *L. pealei* were conducted (Macy 1980). During the first year of the study, the Vovk (1972) method for classifying squid into one of five stages of sexual maturity was used with length-frequency data to characterize changes in the population reproductive structure over time. While the Vovk method was useful, in practice squid were often encountered which could not be readily classified. This report concerns the development and application of a new, faster, and more objective maturity classification system. The method was then successfully employed to classify large numbers of squid throughout the remainder of the study referred to above.

METHODS

From late April through November each year, squid were collected on an approximately biweekly basis throughout the inshore study area located in the southern part of the West Passage of Narragansett Bay, R.I. (inset Fig. 1). A balloon-type otter trawl (Oviatt and Nixon 1973), towed at ca. 4.6 km/h, was used. To insure randomness and adequate size-class representation, samples of at least 100 squid each were randomly selected from the pooled catch of duplicate 20-

[1]Narragansett Mussel Co., 146 Main Street, North Kingstown, RI 02852.

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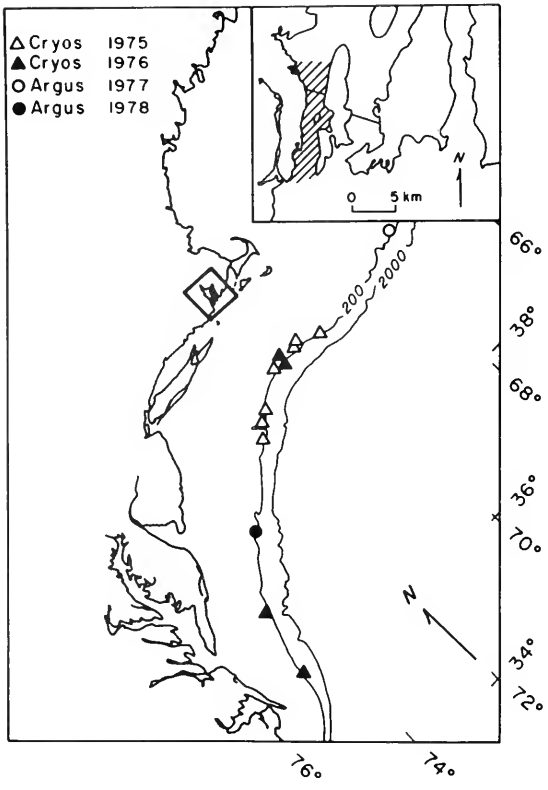


FIGURE 1.—Inshore and offshore sampling locations on the coast and continental shelf of New England. The study area in lower Narragansett Bay is indicated by shading in the inset. Depths in meters.

min trawl tows. The selected squid were bagged and placed in chilled containers for transportation to the laboratory, where they were either immediately examined or were quick-frozen at −25°C for storage. Additional frozen samples of 100-500 squid each were obtained from the National Marine Fisheries Service, Woods Hole, Mass.; from offshore surveys by the French vessel *Cryos* conducted during November-December 1975 and 1976; and from the Russian vessel *Argus* during November 1977 and March 1978 (Fig. 1). Only the 1976 Narragansett Bay and *Cryos* samples were used to develop and verify the classification system described here. The new system was then used to classify the 1977 and 1978 samples.

For analysis, squid were opened midventrally to expose internal organs and allow sexing. Twenty characters were then determined (Table 1). Length measurements were made to the nearest millimeter using a ruler along the greatest dimension, taking care not to stretch the organ or tissue. Frequently, the length of typical spermatophores can be determined while still within Needham's sac or the penis. Mantle width (MW, Table 1), a measure of mantle circumference, was defined as the distance across the widest part of the mantle when opened flat to form a rough isosceles triangle. Mantle thickness (MT) was measured at the thickest portion along the midventral incision. All weight measurements were blotted fresh or live weights (e.g., wet weight, WW, and gonad weight, GW) and were recorded to the nearest 0.01 g if <120 g or to the nearest 0.1 g if >120 g, on a top-loading digital balance. The relative abundance of spermatophores in Needham's sac (ASN), in the penis (ASP), of eggs in the ovary (AEO), or in the oviduct (AEOV) were scored on the basis of "none," "a few," or "many" present. In females, a distinction was also made between immature and mature eggs (Table 1). The four variables—ASN, ASP, AEO, and AEOV— were purposely scored on this nonquantitative basis to avoid time-consuming enumeration. After completing the above length measurements and abundance estimates, the complete reproductive tracts, including gonadal products (Table 1), were dissected out and weighed (GW). From the tabulated raw data the various proportional indices (GI, MWI, MTI, TLI, SPI, NGI, and AGI (see Table 1)) were then computed.

TABLE 1.—The initial 20 input parameters tested for classifying squid into maturity stages. See Figure 3 for organ identification.

Mantle length, cm = DML = dorsal mantle length
Wet weight, g = WW = total live weight
Mantle width, cm = MW
Mantle thickness, cm = MT
Gonad weight, g = GW[1]
Gonad index = GW/WW = GI
Mantle width index = MW/DML = MWI
Mantle thickness index = MT/DML = MTI
Males:
Testis length, cm = TL
Spermatophore length, cm = SPL[2]
Abundance of spermatophores in Needham's sac = ASN[3]
Abundance of spermatophores in penis = ASP[3]
Testis length index = TL/DML = TLI
Spermatophore length index = SPL/DML = SPI
Females:
Nidamental gland length, cm = NGL
Accessory gland length, cm = AGL
Abundance of eggs in ovary = AEO[4]
Abundance of eggs in oviduct = AEOV[3]
Nidamental gland index = NGL/DML = NGI
Accessory gland index = AGI/DML = AGI

[1]For females: (nidamental + accessory + oviducal glands) + ovary/oviduct + eggs.
For males: testis + (Needham's sac + spermatophoric organ + penis).
[2]Length of an average spermatophore excluding tail (= cap thread), scored as "0" if not present or if visible only as a round speck.
[3]Scored on a 1-3 scale, where 1 = none, 2 = "a few," 3 = abundant.
[4]Scored on a 1-5 scale, where 1 = none, 2 = "a few" immature, 3 = many immature, 4 = "a few" mature, 5 = many mature.

Statistical analyses were performed using the Biomed Computer Programs P-Series (BMDP) (Brown 1977) on an Itel AS-5^R computer[2] of the University of Rhode Island Academic Computer Center. The initial data matrix consisted of the 20 variables listed in Table 1, from 675 males and 693 females randomly selected from the 1976 *Cryos* offshore and 1976 Narragansett Bay inshore samples. After standardization of the variables, principal components analysis (BMDP program 4M) (Morrison 1976) was employed to group variables and to determine their importance in accounting for observed variance. Cluster analysis (BMDP 2M) was then used with the Euclidean-distance metric as the amalgamation algorithm to group cases (Anderberg 1973). Finally, stepwise linear discriminant analysis (BMDP 7M) (Anderson 1958) was used with different variable combinations to generate a series of functions which best discriminated between the groups identified in the cluster-analysis stage. A goal of 95% or better overall correct classification of individuals was set.

RESULTS

Development of the Discriminant Functions

The initial cluster analysis revealed only two major groupings for each sex. Further examination, however, suggested that the major clusters consisted of different size-based groupings of mature and immature individuals. Spent squid (using the Vovk (1972) scale) did not group together. Weight variables—WW, GW, and GI (Table 1)—were then dropped from the data matrix because it was known that length measures correlate well with their respective weight counterparts and because principal components analysis had not indicated any particular advantage to using one variable type or the other. Cluster analysis was then rerun using the remaining 17 variables. Four clusters of developmental stages could then be recognized, corresponding to "ripe/spent," "nearly mature," "advanced immature," and "immature" (barely sexable). Several size-based subgroups were still evident within the major clusters. After scoring the squid on a 1-4 scale based on the cluster results, subsequent discriminant analysis produced moderately good separation of the four groups.

Efforts were then focused on improving class separation and reducing the number of variables required. First, those cases which were suspected to be misclassified based on posterior probability and Mahalanobis D^2 statistics (Lachenbruch and Mickey 1968) were corrected. By this time a rather clear picture of the characteristics of each stage had been formed, and thus inspection of the raw data was often sufficient to determine if reclassification was warranted. Using different combinations of variables in the discriminant analyses, the number of variables was further reduced by retaining only those which improved classification accuracy, as indicated by a pseudojackknife test (see BMDP documentation; Lachenbruch and Mickey 1968).

Best results were obtained with the following input variables: MW and MWI, SPL or AGL, API or AGI, TLI or NGI, and ASP or AEOV (Tables 1, 2). In males 94.6% correct classification (Table 2) was obtained using only the three most important variables, SPI, MWI, and TLI (determined by their order of entry into the stepwise analysis), while 96.6% of the females were correctly classified using the first four variables—AEO, AGI, MWI, and NGI. Stage 2 squid were incorrectly classified 19% in males and 10.7% in females, but other squid were correctly grouped in at least 90% of the cases. A plot of the

TABLE 2.—Classification of *Loligo pealei* into stages of sexual maturity using linear discriminant functions. The variables to be measured are listed below with their coefficients or weighting factors for each maturity stage. To classify an individual, construct four linear equations, one for each stage, using the measured values and the appropriate coefficients and constant and solve. The equation resulting in the largest value indicates the stage into which the individual has been assigned.

	Stage			
	1	2	3	4
Variable:				
Males:				
SPI	−949.083	−838.030	−972.007	596.250
MWI	112.680	88.635	92.161	16.472
TLI	7.445	65.620	133.984	130.547
Constant	−49.822	−39.961	−60.416	−35.921
			94.6% correctly classified	
Females:				
AEO	9.695	9.440	13.297	28.915
AGI	−71.476	82.104	233.148	282.733
MWI	98.606	83.025	67.263	76.922
NGI	−26.426	−10.377	54.122	35.443
Constant	−46.310	−37.240	−49.256	−105.526
			96.6% correctly classified	

Example: Assume squid is male.
Then,
$Y(1) = -949.083 \times SPI + 112.680 \times MWI + 7.445 \times TLI - 49.822$

$Y(4) = 596.250 \times SPI + 16.472 \times MWI + 130.547 \times TLI - 35.921$,
where SPI, MWI, TLI are the actual values for the squid in question.

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

mean values of the first and second canonical variates for each stage (Anderson 1958) (Fig. 2) shows that stages 1-4 follow a logical sequence from immaturity to ripeness. The first two canonical variates are the orthogonal pair of linear combinations of the variables which best discriminates between the groups. Mean values for the final discriminant function variables are listed in Table 3. Typical DML's for each of the sex-stage groups have also been included for reference.

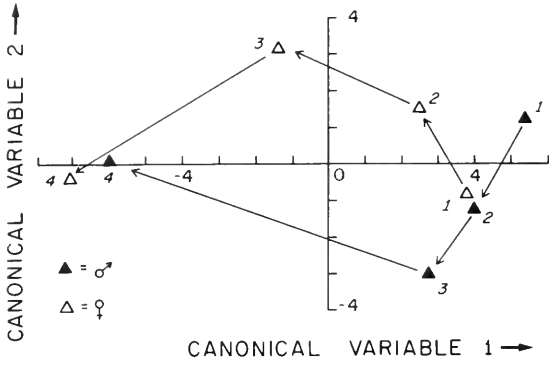


FIGURE 2.—Canonical variates for each stage of sexual maturity evaluated at the stage or group means for each sex. Trajectories between subsequent stages are indicated by arrows.

The Classification Process

To determine the stage of maturation of a squid, the sex must first be determined. If this cannot be done by visual inspection, the squid is considered juvenile (stage 0). Otherwise, DML and MW, plus TL and SPL for males, or NGL, AGL, and EOV for females, should then be determined. From these four or five parameters the appropriate indices needed (Table 2) can be calculated. As indicated in Table 2, a set of four linear equations is then constructed by combining the measured parameter values with the appropriate discriminant function coefficients (weighting factors) and constant listed for each stage. The equation with the largest solution indicates the stage into which the squid should be placed. Thus, once the raw data have been measured and recorded, the actual classification can be done at a later date using even a simple hand calculator. If the raw data are stored on a computer-readable medium, as was done in this study, the process is particularly efficient.

To investigate the broader applicability of the classification, additional squid from the 1976 Narragansett Bay and *Cryos* samples were classified. The discriminant analysis was then performed on these new data to see if the same four stages were identifiable. Over 98% of the individ-

TABLE 3.—Typical mean values (1 SD) of selected maturity stage variables of *Loligo pealei*, listed by sex and stage of development. With the exception of mantle length values (DML), which are from a much larger pooled sample from 1976 to 1978, the reproductive character means are those of the 1976 Narragansett Bay and *Cryos* samples used to compute the final discriminant functions listed in Table 2. Variable coding follows that of Table 1.

	Stage			
	1	2	3	4
Variable:				
Males:				
TLI (%)	11.6 (3.62)	19.0 (3.70)	30.7 (3.73)	30.3 (4.45)
MWI (%)	85.8 (6.90)	71.7 (7.51)	78.0 (8.74)	53.2 (11.71)
SPI (%)	0	0	0	3.6 (0.93)
n	131	119	42	383
DML (cm)	7.1 (2.17)	11.1 (3.25)	10.8 (4.67)	18.6 (8.03)
n	506	610	159	708
Females:				
AEO	1.0	1.0	1.8	4.7
AGI (%)	0	2.6 (1.00)	5.2 (2.62)	5.7 (1.27)
MWI (%)	83.6 (7.98)	74.7 (8.09)	65.0 (11.12)	61.4 (9.25)
NGI (%)	7.8 (3.23)	11.4 (4.86)	24.0 (3.74)	25.8 (4.24)
n	243	124	64	262
DML (cm)	7.8 (2.24)	11.4 (3.09)	13.6 (4.47)	14.3 (3.99)
n	947	467	155	498
Juveniles:				
MWI (%)	97.3 (10.24)			
n	1,857			
DML (cm)	4.6 (1.13)			
n	1,887			

uals of both sexes were correctly grouped, and the new discriminant functions did not differ appreciably from the original ones. Thus the method was shown to be internally consistent (precise). Accordingly, during 1977 and 1978 only the four or five measurements necessary for classification purposes were routinely taken.

The Four Maturity Stages

A description of the general characteristics of each of the four maturity stages of *L. pealei* follows. Figures 3a and b illustrate the important morphometric changes indicated by the discriminant analysis results.

Stage 0: These juvenile squid lack visible gonads (Fig. 3a) and are very broad for their length.

Stage 1: In females (Fig. 3a) the nidamental glands appear as thin white streaks, averaging 8% of DML (Table 3). In males the testis appears as a pale oval body, about 11% of DML, and is frequently obscured by the stomach and caecum.

Stage 2: Both the nidamental glands and testis have almost doubled in length, to 11% and 19% DML, respectively, and the accessory and oviducal glands of females or the spermatophoric organ/Needham's sac complex of males becomes evident. The ovary appears as a fine-grained band of tissue.

Stage 3: This is a transitional stage between immaturity and maturity. The NGI and AGI have approximately doubled again (24% and 5% DML), and the translucent white immature ova give the ovary a distinctly granular appearance (AEO = 2 or 3). The TLI averages 31% DML (Fig. 3b; Table 3), and immature spermatophores may be visible as small white specks in Needham's sac (ASN = 2). No gametes can be found in the penis or oviduct, however.

Stage 4: In these mature squid (Fig. 3b), much of the mantle cavity is occupied by the bulging ovary and oviduct or by the testis. Ripe eggs fill the oviduct and appear as amber spheres 1-2 mm in diameter (AEO>3, AEOV>1). Elongate mature spermatophores (ca. 5 mm long) are visible both in Needham's sac and in the penis (ASN, ASP>1). Immature ova are also found beneath the ripe eggs in the ovary, and usually the spermatophore receptacle is packed with spermatophores. A few virgin females were seen, however.

An Application of the Method

Insights into the usefulness and relevance of the new classification system can be provided by a brief examination of several findings of the overall population study of which this was a part (Macy 1980). Vovk (1972) distinguished between ripe/mature squid and spent squid, but throughout 1975 when the Vovk method was routinely employed, no spent squid were positively identified. Subsequent statistical analysis also failed to make this distinction. Laboratory observations (Macy 1980), however, suggest a reasonable explanation: Isolated females spawned repeatedly over 2-3 wk, but still contained significant numbers of immature eggs; neither sex ceased feeding after mating; and no evidence of nutrient depletion was found. Thus no truly spent individuals might be expected.

Maturing squid, on the other hand, were abundant in late winter prior to the onset of inshore migrations. In the March 1978 *Argus* samples, stage-3 squid constituted 35-40% of the population, while only 8% of the females and 21% of the males had yet reached maturity (stage 4). About 1 mo later (late April) large mature squid began to arrive and spawn in Narragansett Bay. By late July most spawning activity was completed, but already stage-1 individuals from early spawnings were becoming numerically dominant. By the time of arrival offshore, in late fall and early winter (*Cryos* and *Argus* 1977 samples), fewer than 6% of either sex were mature or maturing, but over 50% of the population was composed of stage-2 squid.

These early winter stage-2 squid seem to represent two distinct age/maturity groups: Smaller developing young of the year, and larger and presumably older squid whose gonads appear to be resorbing or regressing. The 1976 *Cryos* sample, for example, consisted of three groups of males with modal lengths of 8.2, 11.6, and 19.1 cm. Only 4.5% of these males ($n = 287$) were mature (stages 3, 4), but 71.4% were at stage 2. The modal size of the stage-2 squid lay between 10 and 12 cm, but individuals ranged from 8 to 23 cm. The remaining stage-1 squid had a modal length of only 8-9 cm. Regressing stage-2 individuals belonged to both the 11.6 and 19.1 cm size classes. Their gonads had the coloration and approximate length of more mature individuals, but were distinctly thin and lacked eggs or spermatophores of any size.

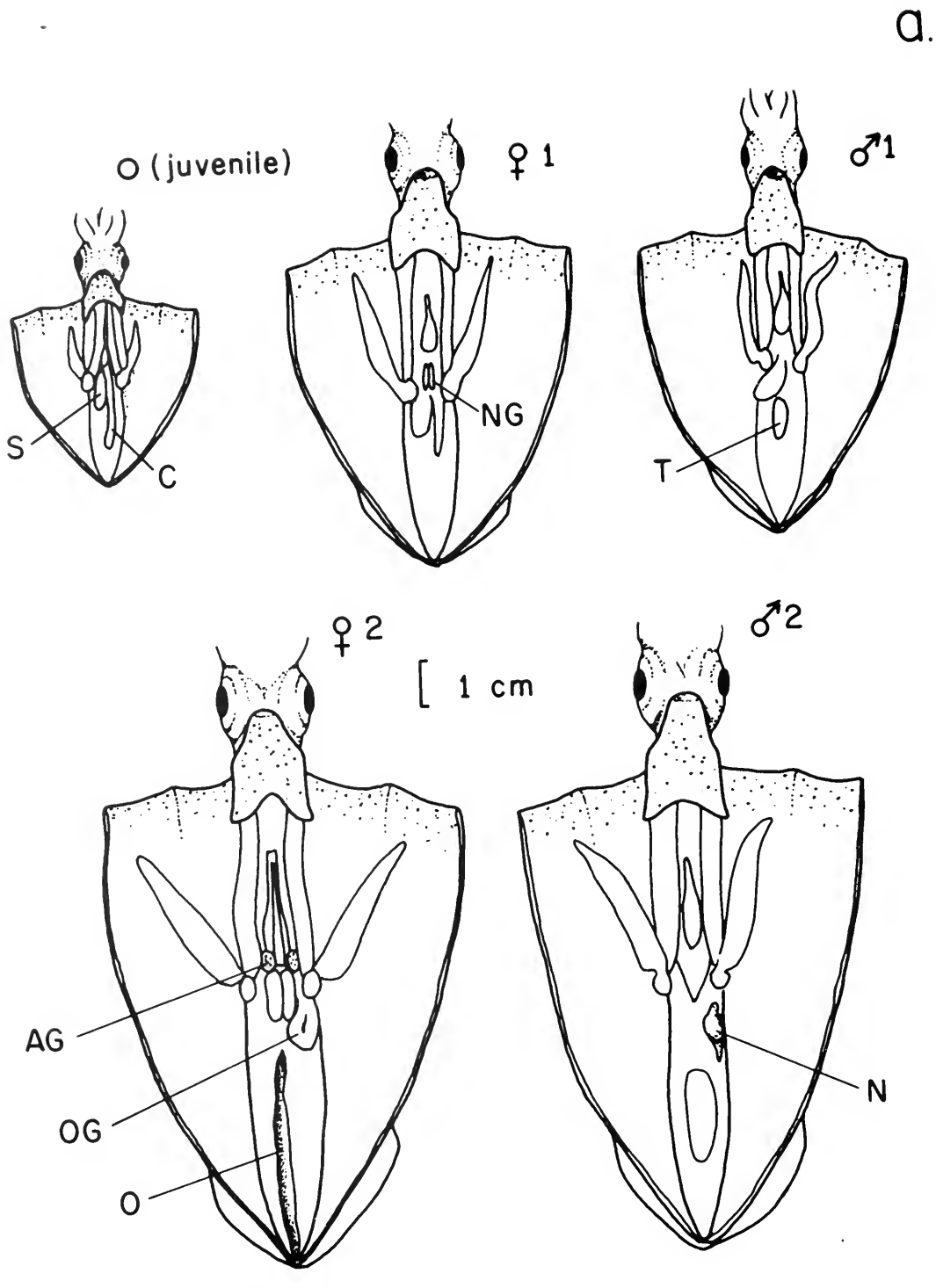
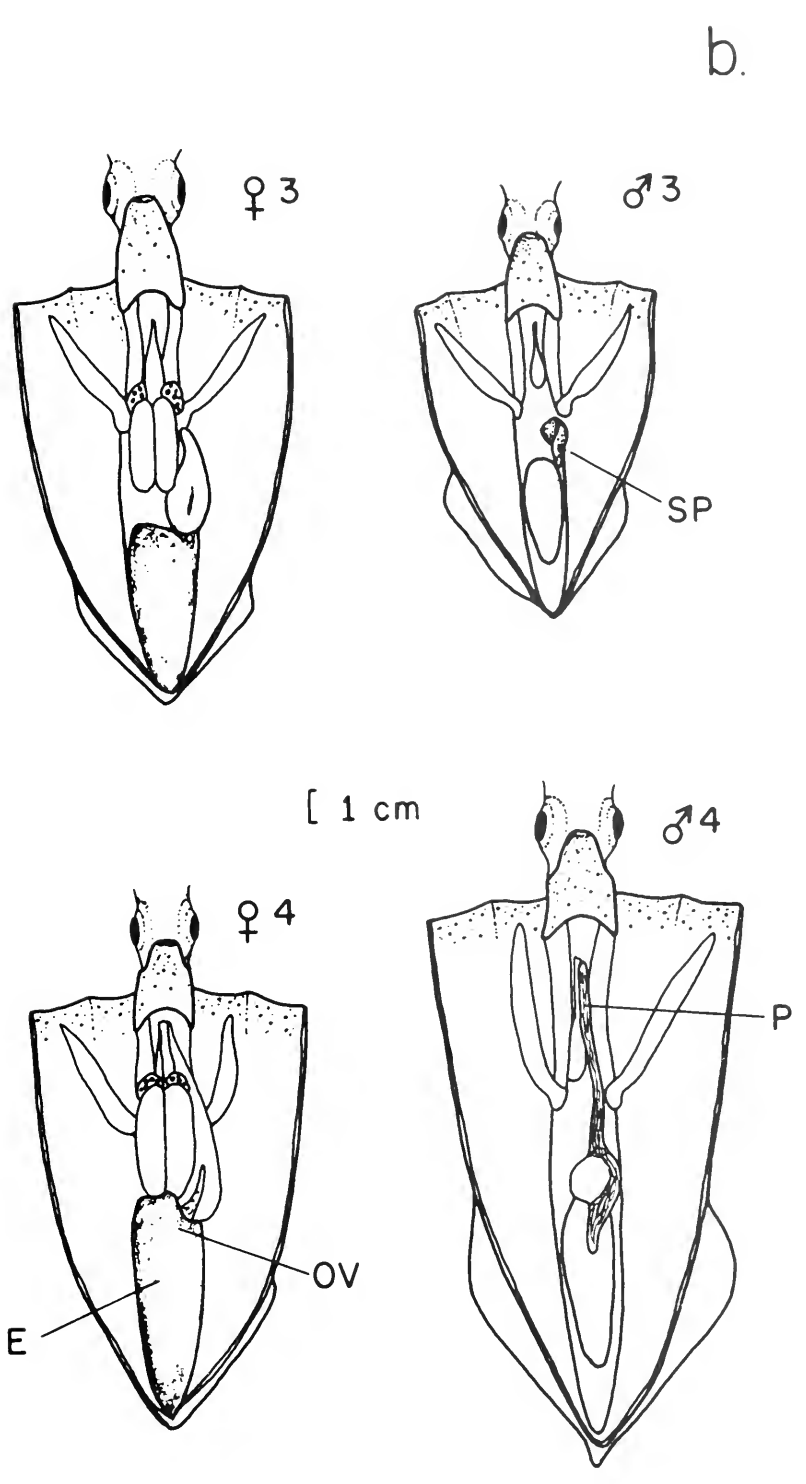


FIGURE 3.—Squid of each stage of maturity illustrating those morphometric changes which the discriminant analysis showed to be important. a, Juvenile and immature squid (stages 1, 2). b, Maturing and mature or ripe squid (stages 3, 4). The diagrams are drawn to scale using the mean values of the morphometric characters given in Table 3 for each sex-stage



combination. S = stomach; C = caecum; NG = nidamental glands; T = testis; AG = accessory glands; OG = oviducal gland; O = ovary; N = Needham's sac/spermatophoric organ complex; SP = spermatophores; E = egg mass (mature); OV = oviduct; P = penis. Digestive tracts are not shown in stages 3 and 4 (Fig. 3b).

DISCUSSION

A classification system should have two major attributes: It should be objective and easy to employ, and it should be biologically meaningful. The major impediment to satisfying both concerns appears to be the high degree of variability which exists within and between populations of *L. pealei*. This species has a wide geographic range, from the coast of South America to Nova Scotia (Cohen 1976), and thus populations living in different parts of the range are exposed to different and varying environmental conditions (temperature, salinity, photoperiod, and food availability) throughout their respective annual cycles. Such environmental variation is manifested by both spatially and temporally varying growth rates, which result in the presence of multiple cohorts within a year class (Summers 1968, 1971; Mesnil 1977; Lange and Johnson 1979), and by differences in the timing of inshore movement and gonad maturation (Hixon 1980; Macy 1980). Thus it is evident that samples used to construct a sexual development classification should at least reflect both the inshore and offshore portions of the range. This was done (Fig. 1). The Vovk (1972) classification, however, was based only on offshore collections, and as a result probably included relatively few spawning individuals and young of the year in early development. Summers (1968, 1969, 1971), on the other hand, sampled both inshore and offshore, but distinguished only between mature and immature individuals.

Objectivity and Utility of the Multivariate Approach

The multivariate approach to the classification problem is appropriate and objective when geographic (environmental) variability of unknown magnitude is superimposed on the usual random variation among individuals, producing the observed age or size and reproductive structure of the population or species. This is true because the analytical approach used here can effectively integrate the information and provide a simple numeric classification rule. Growth rates for *L. pealei* have only been estimated from modal size progressions (Summers 1971; Mesnil 1977), and hence the age of an individual or cohort can only be roughly estimated. Since multiple cohorts occur even within a small area (Narragansett Bay), mean and standard deviation values of morphometric characters, such as of DML or GW, have limited value for discrimination because of the large variability range of individuals (i.e., multimodality). It is known, for example, that considerable variation exists in the age or size of *L. pealei* at spawning (Haefner 1964; Summers 1971; Macy 1980). Standardization by the use of ratio parameters or indices may provide a partial solution to the variability problem.

In the interest of speed and ease of measurement, a set of nominal variables to assess the relative abundance of eggs or spermatophores (ASN, ASP, AEO, AEOV; Table 1) was used in addition to the ratio or interval variables (MWI, TLI, SPI, NGI). The "none," "some," "many" rating scale is not strictly objective, but such coarse evaluations can be done reliably with little training and have proved to be valuable discriminators. Theoretically it is possible to develop an entirely objective classification system. In practice, a somewhat more subjective approach usually proves necessary. What other investigators have found important in distinguishing different maturity groups, such as gonad to body weight ratios (Hayashi 1970), must certainly influence the initial selection of variables to be measured. The investigator must also decide how detailed a classification is desired and what additional parameters may be required. Repeated use of the exploratory technique of cluster analysis followed by stepwise discriminant analysis, as employed here, provides a way of learning how many groups may be present and how to "best" identify them using only those variables which can be shown to significantly aid discrimination. But, at this stage too, the researcher must at least roughly determine the basis for case clustering (by size, color, sexual development, etc.).

Biological Relevance and Accuracy

Statistically accurate and precise results may prove meaningless in reality. Thus the most important verification of the classification scheme is the demonstration of biological relevance in the appropriate context. In each of the 2 yr when the system was routinely employed, a predictable and logical progression of sexual development from hatching to spawning was observed. Moreover, the findings which resulted from this application of the method are reasonable and have significant, broader implications.

Laboratory studies confirm evidence from the field that spent squid cannot be reliably distinguished from spawning squid, even though the majority of samples (Narragansett Bay) were taken on the spawning grounds during the peak of reproductive activity. Hixon (1980) was also unable to find spent *L. pealei* or arrow squid, *L. plei*, in the Gulf of Mexico, and he too documented multiple spawning by *L. pealei*. Furthermore, it has been shown histologically (Burukovski and Vovk 1974) that egg development is highly asynchronous among individuals, and that a series of eggs at different stages of development in the ovary is typical. Prolonged spawning by poorly synchronized individuals of a population would tend to extend spawning over time, and may well account for the lack of reports of dead or dying squid of this species on the spawning grounds.

Stage-3 individuals, particularly males, were poorly sampled during 1976 (Table 3). This was expected since only fully mature individuals move inshore in large numbers, and reproductive development ceases or regresses in late fall. These animals show the first obvious signs of approaching maturity: Developing eggs and spermatophores may be visible, and the nidamental and accessory glands of females and the testes of males (Table 3) have reached sizes comparable to those of fully mature squid. The stage may be of short duration, since gonad development appears to be rapid offshore, with large squid, especially males, maturing faster than the smaller ones (Summers 1969; Macy 1980). In the March 1978 *Argus* samples, large numbers of stage-3 squid were identified, and it is unfortunate that other late winter or early spring offshore samples were not available to better document the latter stages of maturation.

The relatively low classification accuracy of the method for stage-2 squid (81% for males) probably is due to the wide size range of these individuals in the fall and early winter, and to the unusual gonad development of the larger individuals. Sexual regression by gonad resorption to a neutral or inactive state, though relatively common in bivalve molluscs (Sastry 1979), appears to be rare in cephalopods. Regression has been suspected in *L. pealei* (Summers 1971; Vovk 1972; Arnold and Williams-Arnold 1977) and possibly also in European common squid, *L. vulgaris* (Tinbergen and Verwey 1945), however. The phenomenon could explain why only a few of even the largest squid (20 cm and larger DML), thought to be in their second year (Summers 1971; Mesnil 1977), are mature in the late fall and early winter offshore samples. Lacking a reliable means of aging this species, it is not currently possible to prove that the larger "regressed" squid are in fact older than their smaller developing stage-2 counterparts. It is also possible that sexual maturation merely halts at the onset of winter and resumes again in January or February prior to onshore migrations. This hypothesis does not explain why the gonads appear to be shrinking, nor would it account for the presence of both very large and small squid at the same stage of development. Unfortunately, *L. pealei* has not been held sufficiently long in captivity to confirm either supposition.

Comparisons with Other Classification Methods

The main assets of the classification method presented here are its objectivity and its ease and speed of use. To be sure, the development took considerable time, especially interpretation of early cluster analyses, but the basic strategy is relatively straightforward and does have internal accuracy checks. If a more detailed breakdown of the maturation process were desired, e.g., to examine details of gametogenesis, the same analysis techniques could be applied to objectively identify and separate the various phases. Thus the methodology should be applicable to a wide range of biological problems.

When compared with several other classification systems, the advantages of the present method become more evident. Two basic classes of systems exist. Those used by Tinbergen and Verwey (1945), Holme (1974), Juanicó (1979), and Hixon (1980) are mainly qualitative, in that the presence or absence of one or more characters, considerations of color or texture, and estimation of relative sizes or gamete abundance are used. The other group of classification schemes, typified by those of Mangold-Wirz (1963), Hayashi (1970), Vovk (1972), and Durward et al. (1978) are quantitative methods. These schemes may employ one or more subjective judgments or estimates, but rely mainly on objective characters such as relative organ lengths or weights, egg diameters, or spermatophore lengths (absolute or relative) to distinguish successive maturity stages. Both types of classification systems are of value, but only the latter group will be discussed further because their methods are more objective and

perhaps more suitable for large-scale applications.

There are obvious similarities between this classification and that of Vovk (1972), and it appears that, except for stage-5 spent squid, the maturity stages are comparable in both systems. It should be reiterated, however, that the stage characteristics and average parameter values given in this report (Fig. 3a, b; Table 3) were identified after the classification functions had been determined, whereas in the Vovk system the stage indicators form the basis for classification. The offshore squid sampled by Vovk also appear to have been larger by at least 3-5 cm at each stage than those used in this study. Thus, NGL indices in the Vovk study are 6.4-25% greater than those given in Table 3. A TLI, surprisingly, was not used. Vovk did employ hectocotylus length, but in *L. pealei* the hectocotylized arm may be difficult to identify, particularly in small males, and, more important, may be lost or damaged during trawl capture of squid. These and other smaller differences between the methods appear to result mainly because Vovk did not sample the actively spawning inshore population. His method generally works well for experienced personnel, but dissection and weighing of the reproductive tracts and weighing the whole squid take more time and equipment than may be available in the field. At least two more characters must be recorded for each sex as well.

Two simple but objective classifications were developed for Japanese squid, *Todarodes pacificus* (Hayashi 1970) and for female short-finned squid, *Illex illecebrosus* (Durward et al. 1978). Hayashi computed a numerical index, M, equal to the weight of Needham's sac (NW) divided by NW plus the testis weight, or to the oviduct weight (odW) divided by odW plus the ovary weight. If the computed value of M is <0.5, equal to 0.5, or between 0.5 and 1.0, the squid is considered immature, mature, or spent, respectively. Since spent *L. pealei* are at least rare, the system reduces to a two-stage classification which offers no obvious advantage over the immature-mature distinction used by Summers (1968). The dissection and weighing of the two tissues are additional drawbacks.

Durward et al. (1979) used data initially obtained from six *I. illecebrosus* which matured in captivity but had not spawned to develop a five-stage maturity scale for females. These investigators showed (by scatter plots and regression analyses) that relative NGI's correlated well with identifiable stages of ovarian development. Thus only two parameters, DML and NGL, were needed for classification. As Durward et al. have pointed out, the critical values of the NGI for *Illex* for the first four stages are very similar to those for *Loligo* (Table 3). However, in *L. pealei* NGI ranked last of four variables in importance (Table 2), and even the most significant variable (AEO) alone yielded only 77.8% correct classification accuracy. This simple and objective classification for *Illex* is now widely used (Amaratunga and Durward 1979).

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BIOENERGETICS AND GROWTH OF STRIPED BASS, *MORONE SAXATILIS*, EMBRYOS AND LARVAE

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ABSTRACT

Fluctuations in year class size of striped bass are known to be related to development and survival in the early life stages. Bioenergetic aspects of growth and development of striped bass embryos and larvae were determined in the laboratory to discover some of the physiological needs and processes of these stages from fertilization to metamorphosis.

Energy was provided by endogenous (yolk and oil globule) and exogenous (*Artemia* sp.) sources. Initial amounts of yolk and oil varied significantly among eggs from seven different females, and these differences were reflected in different patterns of consumption and growth. Feeding larvae consumed their endogenous oil at rates related to exogenous food intake. Daily food rations of larvae from the onset of feeding to metamorphosis were estimated for field and laboratory conditions. Rations increased with size and age of the larvae. Wild larvae were estimated to have daily rations substantially greater than those of cultured larvae.

Energy outputs were measured in growth and oxygen consumption. Egg size (total dry weight) directly influenced early periods of growth, but later compensatory growth, seen in more rapid growth in larvae from smaller eggs, made up for initial differences. Growth and food consumption were linearly related and, again, different growth characteristics were seen in each batch of fish. Embryos and prefeeding larvae had the highest Q_{O_2}, while metabolism on a weight-specific basis increased with tissue dry weight and was best described by a power function.

Gross caloric conversion efficiencies were highest from fertilization to initial feeding. Feeding larvae used their resources at levels under 20% and their conversion efficiencies did not appear to correlate with food concentration.

In an energy budget model, striped bass embryos and larvae given the highest food density consumed yolk energy at constant rates until totally absorbed. Oil globule consumption fluctuated in relation to growth and nonassimilation, rising sharply after first feeding then declining as food intake increased. Metabolism fluctuated according to developmental stage, rising with the onset of active feeding. Nonassimilation steadily increased as larvae relied more on exogenous food.

Striped bass, *Morone saxatilis*, populations have fluctuated historically throughout their ranges, but in recent years they have declined consistently and unexplainably, especially on the west coast of the United States. Present estimates place the population of the San Francisco Bay/Delta estuary at 33% to 40% of its 1960 peak abundance and it is forecasted to decline further (Stevens 1980). Despite availability of considerable information on striped bass (Pfuderer et al. 1975; Rogers and Westin 1975; Horseman and Kernehan 1976; Setzler et al. 1980), factors that control or influence these fluctuations and declines are not known. Field researchers concluded from 20 yr of data collection that year class size directly correlates with survival and growth during the first 60 d of life and this, in turn, is controlled by environmental conditions—principally the interrelated factors of freshwater flow, water diversion, and food supply (Stevens 1977a, b; Chadwick 1979[2]; Stevens 1980).

To determine the direct causal mechanisms operating between these environmental conditions and early life stage growth and survival, we conducted a series of laboratory experiments over a 6-yr period. Our working hypothesis was that a combination of inherent and environmental factors determined the ability of striped bass embryos and larvae to meet metabolic requirements for successful growth and survival to the pivotal age of 60 d. These factors involve a variety of physiological, morphological, and behavioral functions, and are controlled and/or limited by environmental conditions. Whole organism

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[2]Chadwick, H. K. 1979. Striped bass in California. Prepared for U.S. Environmental Protection Agency, Region II, 27 p.

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bioenergetics was selected as our approach because it represents these functions in an integrated and comprehensive fashion.

Bioenergetics of adult fishes has been studied for some time (Ivlev 1939a, b; Winberg 1956; Warren and Davis 1967; Brett and Groves 1979). As interest in fish eggs and larvae grew, knowledge gained from studies of adults was applied toward research on early life stage energetics (Toetz 1966; Laurence 1969, 1971, 1977; Cooney 1973). Most of these publications are concerned with the critical period when larvae begin active feeding and change from endogenous to exogenous energy sources (May 1974b). Other researchers have used bioenergetic studies to assess the effects of pollutants or other environmental conditions on larvae (Laurence 1973; Eldridge et al. 1977).

Our early research on striped bass embryos and larvae has already been reported (Eldridge et al. 1981). Emphasis was on factors associated with food and feeding of larvae and how they related to mortality, point of no return, development, and, to a limited extent, energetics. The research presented here is a detailed analysis of the energy sources, endogenous and exogenous, and their influence on energy outputs in the early life stages of striped bass.

MATERIALS AND METHODS

Energy Input Determinations

Component analyses of eggs prior to fertilization were done on eggs from seven different females used for embryo and larval studies and on 34 ripe fish collected at random from natural spawning areas. All eggs came from fish from the Sacramento River, Calif. Three replicates of 25 eggs each were weighed fresh after brief blotting on absorbent filter paper, then dried to constant weights at 60°C and reweighed to yield water contents and total dry weights. Yolks and chorions were dissected from Formalin[3]-preserved eggs with microdissection tools; they then were dried and weighed to the nearest 0.1 μg. These amounts were then subtracted from the total weight to provide oil weights. Total lipid contents were obtained by 2:1 chloroform-methanol extraction in micro-Sohxlet apparatus. Our procedure for caloric determinations of yolk and oil involved whole egg homogenization followed by centrifugation to separate yolk, oil, and chorion membrane components. Yolk and oil were then aspirated into dishes, oven dried to constant weights at 60°C, and bombed according to standard microbomb calorimetric methods. Estimates of tissue and *Artemia* caloric contents were made from homogenates of whole animals, the larvae being sampled after complete oil globule consumption. All caloric contents are expressed as calories per gram ash-free dry weight.

All measurements of yolk and oil volume and lengths were done with ocular micrometers in dissecting microscopes. All measurements and determinations were performed at least in duplicate and, if possible, in triplicate.

Eggs from seven different females were fertilized artificially according to methods of Bonn et al. (1976). Eggs were incubated in McDonald jars. After hatching, larvae were transferred to hemispherical 8 l acrylic plastic containers held in water tables to stabilize temperature. Initial stocking densities were approximately 150 larvae/container. In three of the seven batches, larvae were reared to the age when feeding begins, 7 d after fertilization (D-7). The remaining four batches were reared to 29 d after fertilization (D-29). During the process we attempted to duplicate natural water quality conditions as much as possible. Temperatures were maintained at 18°C, and oxygen content was at or near saturation throughout the experiments. Photoperiod and light qualities were kept close to natural. Salinities were zero from fertilization to D-4, 1.0‰ from D-5 to D-13, and 3‰ from D-14 to D-29. Each day containers were cleaned and new water and food were added. An endemic small (1-2 μm) green phytoplankter (*Nephroselmus* sp.) was also added in concentrations of 10^2-10^3/ml.

Larvae began feeding consistently on D-7, at which time they were given newly hatched, live *Artemia salina* nauplii (San Francisco Bay Brand). The range of initial food concentrations was selected to include the estimated natural zooplankton densities (0.003 to 0.010/ml (Daniel 1976)) and the concentrations used in other striped bass research. Initial concentrations were 0.00, 0.01, 0.10, 0.50, 1.00, and 5.00 *Artemia*/ml.

To estimate daily exogenous food rations of larvae we used the following formula: daily food ration = (average stomach contents)(hours of active feeding)/digestive time. Detailed studies

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

on diel feeding patterns and evacuation rates of larvae in our experimental systems were conducted in the early stages of this study and were presented in Eldridge et al. (1981). Because larvae in all food concentrations consumed their food within 10 h after food was first introduced, we selected 10 h/d for use in the above formula. We found that sampling larval stomachs 1 h after food introduction was most representative of average stomach contents during the active feeding periods. A minimum of 10 larvae was dissected and the stomach contents were quantified for each food ration estimate for each experiment. Evacuation rates of food ingested by larvae which were feeding continuously ranged from 1.5 to 5.5 h with an overall average of 3.3 h. Times of 100% evacuation were combined for different-aged larvae and used in this study (Table 1).

TABLE 1.—Average times (h) required for *Artemia* nauplii to pass through the digestive tracts of continuously feeding striped bass larvae.

Age (days after fertilization)	Food concentration (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9-16	3.3	4.0	3.5	4.5	4.0
17-24	2.5	2.8	3.5	3.5	2.3
25-29	2.5	2.5	3.7	4.0	3.0

Energy Output Determinations

Growth of embryos and larvae was measured by carefully removing all yolk and oil globules from Formalin-preserved specimens, rinsing the remaining tissues in distilled water, drying at 60°C, and weighing to the nearest 0.1 μg. Measurements were in duplicate with 3 to 5 specimens per sample. Standard lengths of larvae were measured to the nearest 0.1 mm with an ocular micrometer. Duplicate measurements of 20 larvae each were done. Preserved specimens were measured as soon as possible. The entire set of samples from each experiment required an average of 8 wk to process.

Oxygen consumption was used as a measure of "routine" metabolism (Fry 1971) and was measured with standard manometric techniques using a differential microrespirometer. At least five replicate samples (from 5 to 50 animals/sample depending on age and size) were taken at each test period. Sampling occurred at D-0.5, -1.0, -2.0, -4.0, and on each even day until D-30 (time measured from time of fertilization).

RESULTS

Energy Inputs

Endogenous Sources

Initial sources of energy for striped bass embryos and early larvae are yolk and oil, the latter contained in a single large globule. The relative composition of these egg components was found to vary considerably between the seven different females used in rearing experiments (Table 2). Oil accounts for most of the variability in dry weight, whereas yolk is more variable in measurements of volume. Caloric contents of these two energy sources were consistent, which indicates that variability of total energy in the egg results from differences in absolute amounts of oil, yolk, or both, rather than differences in the energy content of those materials. Eggs from different females contained widely ranging

TABLE 2.—Dry weights, volumes, and caloric contents of striped bass eggs and egg components at time of fertilization. Three replicates of 25 eggs each were used for dry weights, three replicates of 20 eggs each for volumes, and two replicates of approximately 50 mg (dry weight) were used for caloric content determinations.

Experiment no.	Mean dry weight (mg)				Mean volume (mm^3)		Caloric content				
							yolk		oil		total
	yolk	oil	chorion	total	yolk	oil	cal/g	cal/egg	cal/g	cal/egg	cal/egg
1	0.114	0.150	0.022	0.286	0.67	0.21	5,687	0.648	9,223	1.383	2.031
2	0.089	0.137	0.023	0.249	0.65	0.20	5,720	0.509	9,360	1.282	1.791
3	0.131	0.089	0.028	0.248	0.57	0.13	5,622	0.736	9,133	0.813	1.549
4	0.106	0.251	0.016	0.373	0.52	0.21	5,641	0.596	9,869	2.477	3.073
5	0.118	0.189	0.014	0.321	0.20	0.17	5,635	0.665	9,627	1.819	2.484
6	0.089	0.128	0.014	0.231	0.38	0.18	5,635	0.502	9,738	1.247	1.749
7	0.083	0.115	0.012	0.210	0.62	0.14	5,625	0.467	9,655	1.110	1.577
$\bar{x}$	0.104	0.151	0.018	0.274	0.516	0.177	5,652	0.589	9,515	1.447	2.036
SE	0.018	0.054	0.006	0.057	0.170	0.033	37	0.100	278	0.546	0.558
Range	0.089–0.131	0.089–0.251	0.012–0.028	0.210–0.373	0.20–0.67	0.13–0.21	5,641–5,720	0.467–0.736	9,133–9,869	0.813–2.477	1.549–3.037
C.V.	17.3	35.6	33.0	20.8	33.0	18.4	0.7	16.9	2.9	37.7	27.4

amounts of yolk and oil (coefficients of variation 27% and 25% for yolk and oil, respectively) and little (<3%) difference was found in energy contents. The oil globule accounted for an average 55% of the dry weight and 71% of the total energy of the egg. Yolk accounted for 38% of dry weight and 29% of energy. The two sources combined provided an average 2.036 cal/egg.

Yolk contained an average 5,652 cal/g, which agrees with Phillips' (1969) estimate of 5,660 cal/g gross energy for digested protein. Lipid extraction analyses of yolk from three of the seven spawned females showed that only 3.8% of dry weight was lipid material.

Embryos and larvae from the seven different females consumed their yolks linearly (Fig. 1). At hatching an average 58% of the original yolk energies remained, and they were totally utilized between D-6 and D-7, the time when active feeding began. Analyses showed no significant differences in yolk utilization rates but highly significant differences in intercepts ($P \leq 0.01$), further indication of the differences in original yolk reserves.

Initial oil energy contents per egg ranged from 0.8 to 2.5 cal (Table 2) and differed significantly between batches ($P \leq 0.05$). An average 86% of these initial amounts remained at hatching and 71% was present on D-7. Analyses of covariance indicated that the utilization rates from fertilization to feeding (Fig. 2) also were significantly different ($P \leq 0.05$). With the exception of one batch, embryos and larvae consumed their oil energies so that approximately the same amounts of energy remained on D-7.

The rates at which oil globule calories were utilized and the ages at complete oil energy absorption (D-20 to D-29) appeared related to food concentration (Fig. 3). Starved larvae and those in 0.01 *Artemia*/ml concentrations conserved oil, whereas those fed progressively higher concentrations consumed energy at faster rates. Analyses of covariance showed significant differences in oil consumption among batches within each food concentration. Tests of food concentrations and oil consumption within batches showed all to have highly significant differences ($P \leq 0.01$) in intercepts, and two of the four batches had significant slope differences ($P \leq 0.05$).

Exogenous Sources

Larvae in all experiments began active feeding 5 d after hatching. Average stomach contents, presented as the average number of ingested *Artemia* and their equivalent calories, are presented in Table 3. These data were further used to calculate daily food rations (Table 4). With some exceptions, larvae increased their exogenous energy intake in direct relation to food availability and age in all food concentrations except 0.01 *Artemia*/ml. Larvae in this low concentration showed no particular trend.

Energy Outputs

Growth

Embryonic and prefeeding larval growth, measured in assimilated tissue calories, differed significantly among the seven batches ($P \leq 0.01$).

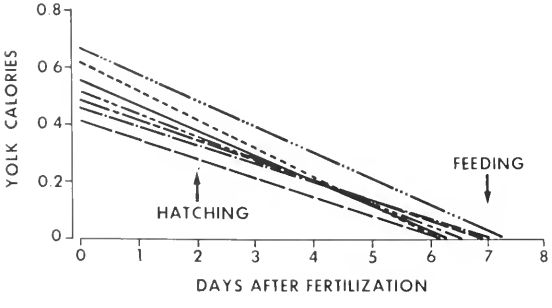

FIGURE 1.—The consumption of yolk calories by seven different batches of striped bass embryos and larvae cultured under identical conditions.

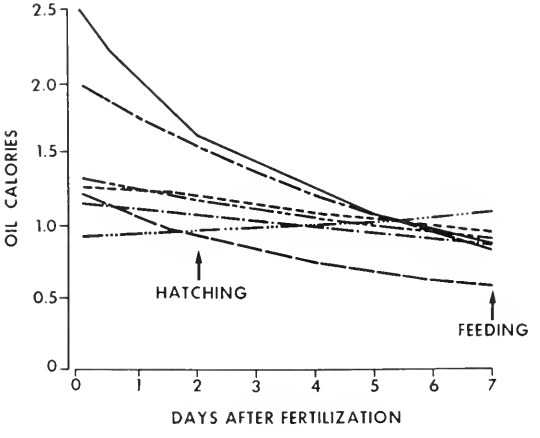

FIGURE 2.—The consumption of oil globule calories by seven different batches of striped bass embryos and prefeeding larvae.

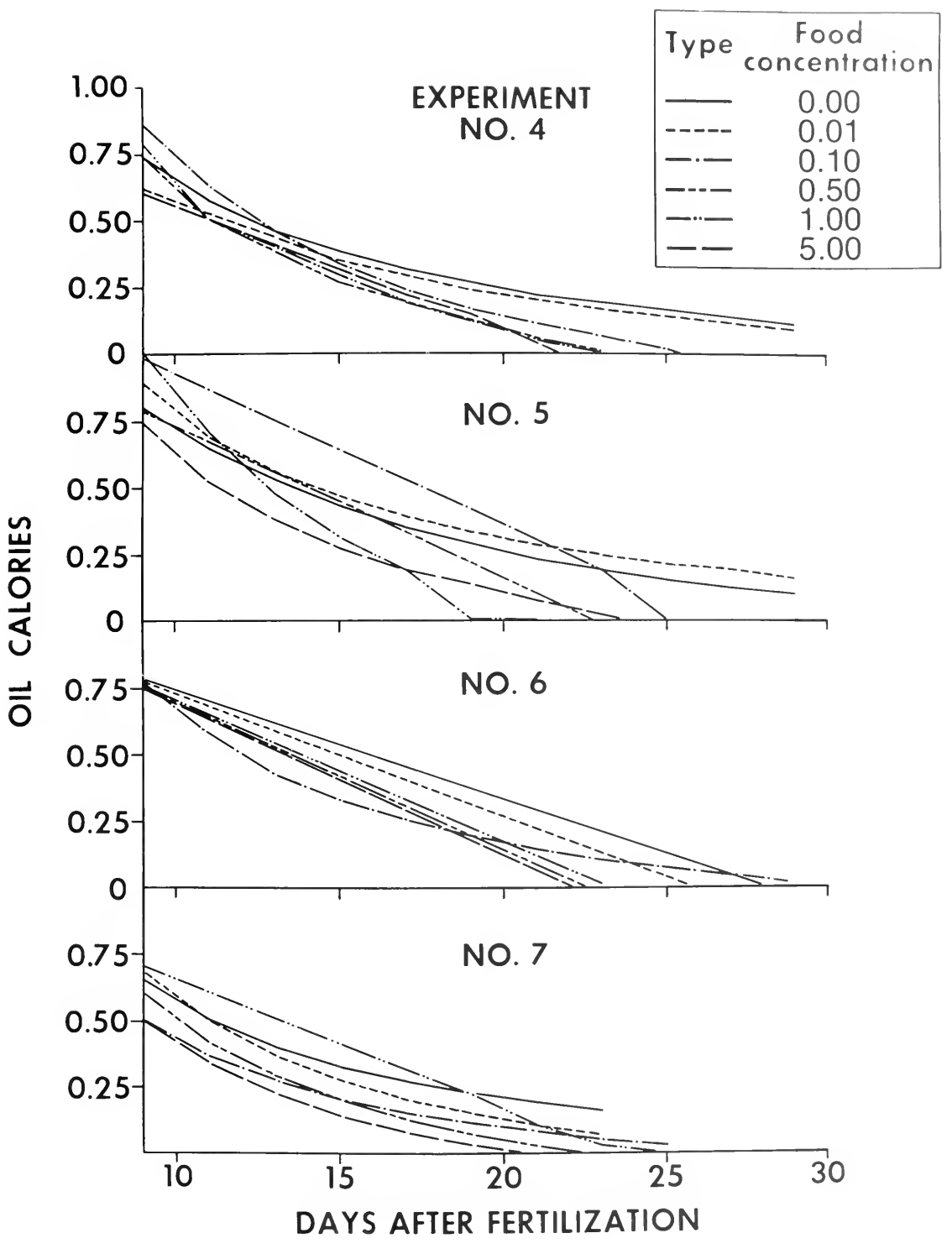

FIGURE 3.—The consumption of oil globule calories by striped bass larvae from four different batches (experiments 4-7) fed six different food concentrations (0.00 to 5.00 *Artemia*/ml).

TABLE 3.—Average stomach contents and their corresponding caloric equivalents of striped bass larvae feeding at different food concentrations from 9 to 29 d after fertilization. Presented as number of food organisms/number of calories per larva.

Age (days after fertilization)	Food concentrations (no. *Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.05/0.001	0.15/0.001	5.40/0.052	4.30/0.041	7.60/0.073
11	0/0	0.85/0.008	7.50/0.072	11.70/0.112	2.80/0.027
13	1.50/0.014	3.30/0.032	9 20/0.088	18.40/0.177	9.890/0.094
15	0.05/0.001	4 10/0.039	23.10/0.222	24.00/0.231	10.20/0.098
17	0.15/0.001	8.40/0.081	27.10/0.260	39.40/0.39	18.60/0.179
19	0/0	12.50/0.120	29.50/0.283	33.30/0.320	24.60/0.236
21	0.15/0.001	13.00/0.125	26.10/0.251	40.00/0.384	33.70/0.324
23	4.16/0.040	14.20/0.136	47.40/0.456	35.90/0.345	53.00/0.509
25	1.10/0.001	57.20/0.550	17.00/0.163	83.10/0.799	59.40/0.571
27	0.25/0.002	470/0.045	65.40/0.628	60.20/0.579	72.40/0.696

TABLE 4.—Estimated daily food ration (number of *Artemia* consumed by one larva in 24 h/equivalent calories consumed in 24 h) of striped bass larvae at different ages feeding at different food densities.

Age (days after fertilization)	Prey densities (*Artemia*/ml)				
	0.01	0.10	0.50	1.00	5.00
9	0.2/0.001	0.4/0.004	15.4/0.148	9.6/0.092	19.0/0.183
11	0/0	2.1/0.020	21.4/0.206	26.0/0.250	7.0/0.067
13	4.6/0.044	8.3/0.079	26.3/0.253	40.9/0.393	24.5/0.235
15	0.2/0.001	10.3/0.099	66.0/0.634	53.3/0.513	25.5/0.245
17	0.6/0.006	30.5/0.294	77.4/0.744	112.6/1 082	82.7/0.794
19	0/0	45.5/0.437	84.3/0.810	95.1/0.914	109.3/1.051
21	0.6/0.006	47.3/0.454	74.6/0.717	114.3/1.098	149.8/1.439
23	16.6/0.160	51 6/0.496	135.4/1.301	102.6/0.986	235.6/2.264
25	1.0/0.010	18.8/0.181	176.8/1.699	150.5/1.446	241.3/2.319
29	11.6/0.111	58.8/0.565	194.3/1.867	288.8/2.775	410.0/3.940

Greater differences were seen in the intercepts than rates, and this, in turn, seemed related to the initial egg sizes (total dry weights). Descriptive equations for assimilated tissue calories of the different experiments are in Table 5. Daily growth coefficients (Laurence 1974) to hatching and to first feeding correlated well with initial egg size. The rate of growth from fertilization to hatching age (avg. $G_W = 1.872$) was three times that to feeding age (avg. $G_W = 0.647$).

Standard lengths at hatching (3.9±0.6 mm), and especially at first feeding (5.8±0.3 mm) (Table 5), also correlated well with initial egg size. Smaller standard deviation of D-7 larvae than of newly hatched larvae (coefficients of variation 5% vs. 15%) suggests larval lengths converged with age.

Growth characteristics of feeding larvae were unique to each batch within each food concentration as was found in earlier stages. Examples are given in Figures 4 and 5 which present growth in tissue calories and standard lengths of larvae fed the high food ration (5.0 *Artemia*/ml).

Within each batch, growth was linearly related to food concentration (Fig. 6). Differences in overall growth are again apparent. Experiment 7 larvae grew fastest.

Larval length-weight relations were exponen-

TABLE 5.—Best descriptive equations (y = tissue calories, x = days after fertilization), initial egg dry weights, standard length, and growth coefficients of striped bass embryos and prefeeding larvae.

Experiment	Initial egg size (μg)	Best fit growth equation (tissue cal)	Standard errors of estimate	Standard lengths (mm)		Daily instantaneous growth coefficients[1]	
				at hatching	at feeding	to hatching	to feeding
1	286	$y = 0.159359\ (x^{0.578582})$	0.0480	4.7	5.5	1.966	0.624
2	249	$y = 0.107496\ (x^{0.847938})$	0.0653	4.0	5.6	1.844	0.630
3	248	$y = 0.133695\ (x^{0.860384})$	0.0446	4.7	5.7	1.733	0.694
4	373	$y = 0.139619\ (x^{0.732174})$	0.0537	3.2	6.1	2.172	0.715
5	321	$y = 0.190165\ (x^{0.767811})$	0.0537	3.2	6.1	2.172	0.715
6	231	$y = 0.090892\ (x^{0.828853})$	0.0187	3.6	5.9	1.763	0.633
7	210	$y = 0.115968\ (x^{0.692893})$	0.0763	3.7	5.4	1.733	0.580

[1]Daily instantaneous growth coefficients = $\log_e W$/days after fertilization where W = dissected tissue dry weight in micrograms.

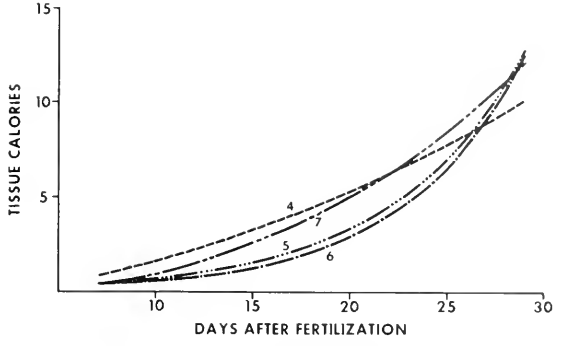

FIGURE 4.—Growth of four batches of feeding striped bass larvae measured in calories of assimilated tissue from first feeding (D-7) to D-29.

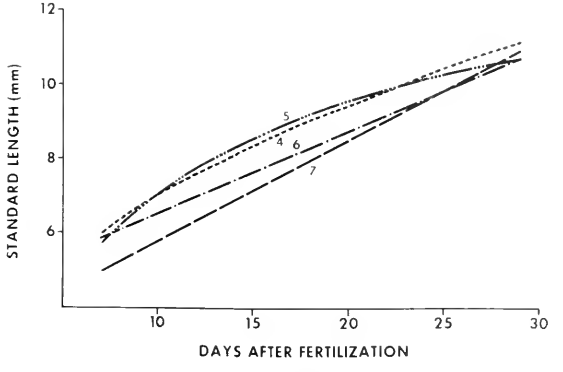

FIGURE 5.—Growth of four batches of feeding striped bass larvae measured in standard lengths from first feeding (D-7) to D-29.

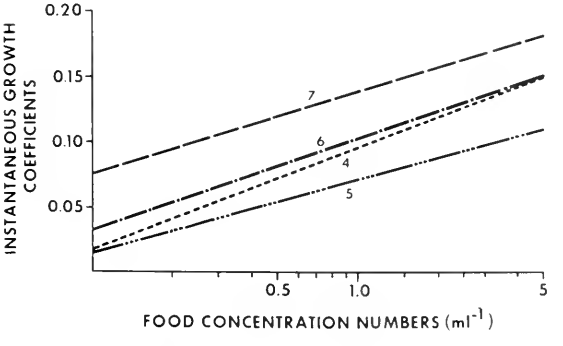

FIGURE 6.—Instantaneous growth coefficients of four batches of feeding striped bass larvae that fed on six different food concentrations (0.00 to 5.00 *Artemia*/ml).

tial for all fish groups (Fig. 7). Experiment 7 larvae were the heaviest per unit length and did not attain the lengths that other larvae did. All larvae put on weight rapidly after reaching a standard length of about 8 mm.

Oxygen Consumption

Metabolic rates of embryos and larvae are presented in Figure 8. Embryos and prefeeding larvae had the highest Q_{O_2}'s. After feeding began oxygen consumption stabilized and remained constant for the duration of the experimental period. On a weight-specific basis oxygen consumption increased with tissue dry weight and was best described by a power function (Fig. 8), although the relationship appears almost linear.

Utilization Efficiency

Gross caloric conversion efficiencies were highest from fertilization to initial feeding, followed closely by efficiencies during the embryonic period (Table 6). Only in larvae from the highest food concentration did conversion efficiencies remain at elevated levels. Larvae feeding at the other food concentrations used their resources at levels under 20%, and their conversion efficiencies did not appear to correlate with food concentration. Starved larvae had the lowest efficiency and demonstrated negligible growth after D-7.

TABLE 6.—Mean gross caloric conversion efficiencies (in percent) for striped bass embryos, prefeeding larvae, and larvae feeding at different prey concentrations.

To hatching	To initial feeding	Food concentrations (*Artemia*/ml) to 29 d after fertilization					
		0.00	0.01	0.10	0.50	1.00	5.00
37.7	43.8	15.0	19.0	13.9	17.3	18.7	31.9

DISCUSSION

Energy Inputs

Striped bass eggs were found to be high in energy content and to vary considerably in size. Undoubtedly the high proportion of lipids (found mostly in the oil globule) makes the striped bass egg one of the most energy-rich of fish eggs. At 7,808 cal/g striped bass eggs exceed the caloric values of eggs from freshwater, anadromous, and marine fishes which normally range from 5,386 to 6,238 cal/g (Hayes 1949; Smith 1957,

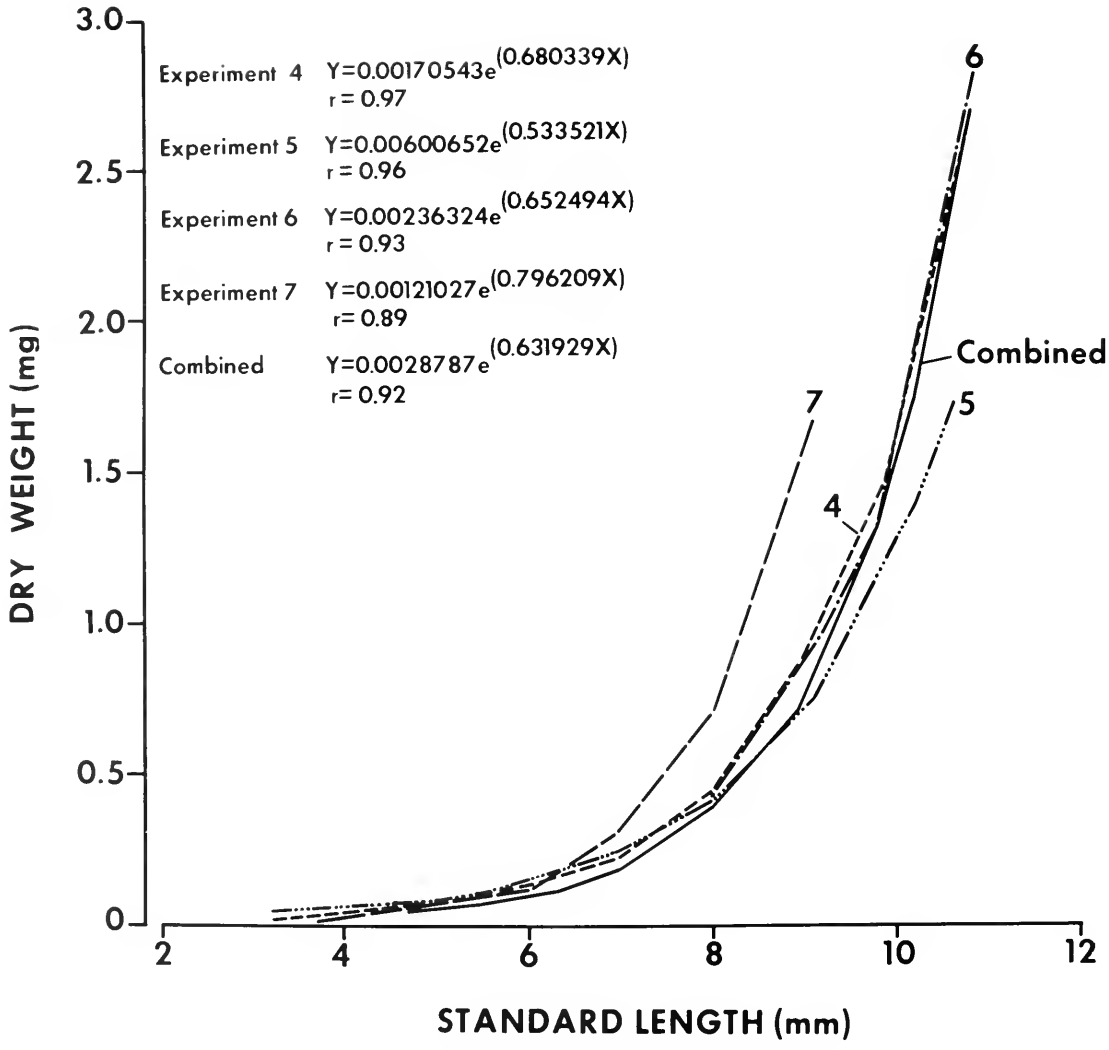

FIGURE 7.—Assimilated tissue dry weights and corresponding standard lengths of four batches of striped bass larvae.

1958; Flüchter and Pandian 1968; Blaxter 1969). Egg size variability was not unexpected as eggs are reported to vary within and among a variety of fish species (*Clupea harengus*, Blaxter and Hempel 1963; *Sardinops caerulea*, Lasker 1962; *Trachurius symmetricus*, Ware 1975; Theilacker 1980[4]).

It appears from studies of embryos and larvae with large oil globules that the energy from the oil is important to larval growth and survival, and the influence of this energy source is present for long periods. In this study and that of Rogers and Westin (1981), striped bass larvae retained their oil energy reserves for extended periods, especially when starved. This is not common in fishes although similar retention of the oil globule was noted in *Bairdiella icistia* (May 1974a) and *Leuresthes tenuis* (May 1971; Ehrlich and Muszuski in press). The oil globule also seemed to help striped bass larvae avoid or prolong the typical point-of-no-return, the time of irreversible starvation (Eldridge et al. 1981). In a review of larval fish physiology, Theilacker (1980) concluded that in addition to egg size and activity, egg lipid level relates most to larval resilience.

[4]Theilacker, G. H. 1980. A review of pelagic larval fish behavior and physiology. Presented at Institute del Mar del Peeru (IMARPE) Workshop, April 21-May 5, 1980.

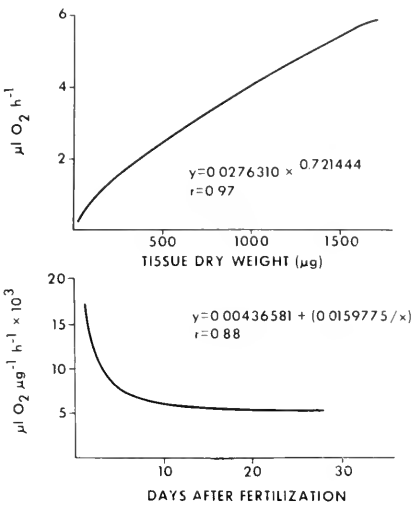

FIGURE 8.—Oxygen consumption of striped bass embryos and larvae plotted against assimilated tissue dry weight (above) and age (below).

In an attempt to compare our laboratory derived estimates of daily food ration with those from wild striped bass larvae we obtained stomach content data of 1,468 field-caught larvae (sized to 11.9 mm SL) spawned from 1971 to 1973. The summarized data of Table 7 show wild larvae were smaller (4.0 to 4.9 mm) than laboratory larvae (6.1 mm) at the time of first feeding. This is possibly due to differences in preservation methods. When wild larvae attained sizes of 7.0 to 7.9 mm, over 75% were feeding. This agrees with our laboratory observation that over 80% of the 2-wk-old and older larvae (>7.0 mm SL) fed actively in food concentrations of 0.50 *Artemia*/ml and greater. The overall average of feeding incidence for wild larvae was 70.5%. Wild larvae also displayed preference for cladocerans, *Cyclops* sp. and *Eurytemora* sp., which, together, accounted for 89% of all food consumed. Other studies of striped bass from east coast nursery areas showed that the largest part of the larval diet consisted of small crustacea and microplankton (Meshaw 1969; Humphries and Cumming 1972).

Using these data we calculated daily caloric rations, according to the previously described formula, for each size category of wild larvae (Table 7). Caloric equivalences for the different food types were obtained from the literature (Richman 1958; Cummins 1967; Clutter and Theilacker 1971; Laurence 1976; Sitts 1978). In-

TABLE 7.—Average feeding incidences, stomach contents by food item, equivalent caloric values, and calculated daily caloric rations of 1,468 striped bass larvae collected in the San Francisco Bay/Delta estuary during 1971-73. The last column presents laboratory-derived average caloric rations for larvae of comparable sizes.

Larval size (mm SL)	% with food in stomachs	Neomysis	Coropphium	Cladocerans	Cyclops	Diaptomus	Eurytemora	Acartia	Harpacticoids	Misc. copepods	Total caloric equivalent	Estimated daily ration (cal)	Laboratory derived average ration (cal)
3.0-3.9	0	0	0	0	0	0	0	0	0	0	0		—
4.0-4.9	16.1	0	0.01	0.29	0.18	0	0.24	0.01	0.03	0.01	0.107	0.646	—
5.0-5.9	32.6	0.02	0.09	0.82	0.60	0	0.28	0.01	0.01	0.01	0.299	1.801	—
6.0-6.9	57.5	0	0.10	0.80	0.81	0.01	0.38	0.01	0.01	0.01	0.317	1.910	0.183
7.0-7.9	76.7	0.02	0.11	0.82	1.00	0.01	0.49	0.01	0.02	0.01	0.357	2.152	0.151
8.0-8.9	80.9	0.04	0.14	0.97	1.22	0.01	0.63	0.01	0.02	0.01	0.436	2.627	0.520
9.0-9.9	84.7	0.09	0.18	1.08	1.25	0.01	0.68	0.01	0.03	0.02	0.496	2.989	1.245
10.0-10.9	85.3	0.16	0.22	1.31	1.27	0.04	0.82	0.01	0.01	0.02	0.599	3.609	2.607
11.0-11.9	82.9	0.19	0.28	1.51	1.37	0.02	0.92	0.01	0.02	0.01	0.689	4.151	N A

formation on natural feeding duration was taken from Miller,[5] which showed that wild larvae feed 24 h a day but feed more intensely during crepuscular periods. Evacuation rate was set at 5 h, a compromise between our estimate of 3.3 h for larvae fed *Artemia* at 18°C and the estimate of 11 to 12 h made by McHugh and Heidinger (1977) for larvae given *Artemia* and held at 25°C. Daily caloric rations for wild larvae range from 0.646 cal for smaller larvae to 4.151 cal for 11.0 to 11.9 mm SL larvae. These rations are higher than those of laboratory larvae. Except for the largest cultured larvae, rations were usually one-half the field larvae rations. Thus within equivalent size categories wild larvae appear to have daily rations substantially greater than those of cultured larvae. Other estimates of daily rations of striped bass larvae range widely. Miller (footnote 5) concluded that field-caught larvae (6.8 to 9.2 mm SL) consumed rations equivalent to 0.159 cal for rotifers or up to 2.958 cal for cladocerans. Doroshev (1970) estimated daily intake of laboratory-reared larvae to be 9.704 to 29.112 cal, consisting of *Cyclops* nauplii or small copepods. Our average calculated daily estimates for the different food concentrations for the 29-d experimental period fall within Miller's estimates of wild larvae (Table 8).

TABLE 8.—Mean daily caloric rations of striped bass larvae given five different food densities from D-7 to D-29.

Food density (*Artemia*/ml)	Mean overall daily caloric ration (calories/larva per d)
0.01	0.035
0.10	0.439
0.50	0.802
1.00	0.823
5.00	1.313

Energy Outputs

Our results suggest that there is compensatory growth in embryos and larvae that offsets initial egg size differences. The size ranges are not as broad in newly hatched larvae and larvae at first feeding (D-7) (seen in Table 5) as they are in the eggs. Likewise, initial egg size corresponds better to the size ranking of larvae at hatching age than it does to larvae at feeding age. The mean instantaneous growth coefficient during the 2-d embryonic period was 1.872 with a coefficient of variation (C.V.) of 8.5% (Table 5). From hatching to first feeding it was 0.647 with a decreased C.V. of 7.0%, an indication of narrowing diversity. Further compensatory growth was seen in tissue weights and standard lengths of feeding larvae (Figs. 4, 5), and convergence of sizes was seen in all food concentrations above 0.10 *Artemia*/ml. Weights were similar on D-25 and lengths on D-27. In the two higher food concentrations, sizes converged by D-17. Compensatory growth was documented years ago in salmon fry (Hayes and Armstrong 1942), so this is not necessarily unique to striped bass. Theilacker (in press) more recently found that growth rates of jack mackerel larvae varied with egg size.

Growth of feeding striped bass larvae was clearly tied to exogenous food consumption as seen in Figure 6. This relation is well established in other larval fishes (O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; May 1974a; Houde 1977; Taniguchi in press).

Growth rates of our larvae, especially those in the higher food concentrations, are similar to findings with other populations of striped bass (Rogers et al. 1977). The most comparable study (Daniel 1976) included continuous introduction of *Artemia* for 10 d in concentrations of 0.004 to 0.030 nauplii/ml. Twenty-five days after hatching larvae grew to an average standard length of 8.5 mm. Fish used in the present study were longer than Daniel's in the two higher food concentrations and smaller in the three lower concentrations. As in our study, Daniel's larvae also grew directly in relation to food density. Tissue weights of Daniel's fish fed the 0.008 and greater *Artemia*/ml concentrations approximated those of our fish fed concentrations of 0.005 and above. Our larvae that fed at 5.0, however, were all heavier than Daniel's larvae. Lal et al. (1977) also cultured California striped bass larvae but in varying salinities. Larvae of comparable age feeding on *Artemia* (densities unreported) were similar to our larvae from the 0.50 nauplii/ml. Larvae from our higher densities were larger.

Oxygen consumption measurements varied directly with size, age, and temperature. Because temperature was held constant in all tests, age and size were the most influential factors affecting oxygen consumption, and these factors produced distinctive patterns. The high metabolic rates (Q_{O_2}'s) demonstrated by embryos and newly hatched larvae were probably the results of the activity accompanying hatching and of the high metabolic needs associated with rapid tis-

[5]Miller, P. E., Jr. 1978. Food habit study of striped bass post yolk-sac larvae. The Johns Hopkins University, Chesapeake Bay Institute, Spec. Rep. 68, Ref. 78-8.

sue growth and differentiation. These needs remained high into the period of feeding transformation and then leveled off to nearly constant rates after D-10. Similar patterns have been seen in other fishes (Smith 1957; Blaxter 1969). The relation of oxygen consumption to weight is usually described in a log-log transformation with a slope approximating 0.8 (Winberg 1956). Our slope of 0.72 shows that our equation describes the weight-metabolism relation up to the final size encountered. Laurence (1977) found winter flounder metabolism profoundly changed after metamorphosis resulting in a curvilinear pattern described best by a third degree polynomial equation. It is likely that striped bass would show similar tendencies when measured further along in development.

Reviews (Blaxter 1969; Eldridge et al. 1977) show that efficiencies during the strictly endogenous energy period of embryos and prefeeding larvae ranged from 40% to 70%. Our findings with striped bass tended toward the low side of this range. *Micropterus salmoides* was most similar to striped bass, with efficiencies of 35.2% to hatching and 43.9% to feeding (Laurence 1969). Like those of striped bass, the eggs of *M. salmoides* also possess large oil globules, and their larvae have similar predatory behavior. Gross growth efficiencies of aquatic consumers in general normally fluctuate between 15% and 35% (Welch 1968). Efficiencies of larval and postlarval fishes have also been found to be within this range (Ivlev 1939a; Laurence 1973, 1977). Ivlev (1945) believed postembryonic stages were restricted to efficiencies <35%, and fish normally have decreasing efficiencies with age (Parker and Larkin 1959; Theilacker footnote 4). All our efficiency values support these conclusions. Whether feeding or not, our older larvae had lower conversion efficiencies, probably resulting from increased metabolic demands associated with greater activity.

All organisms must balance input and output energies to successfully survive, grow, and ultimately reproduce. The essential relations between input and output energies and the equation which balances them have been well discussed by several authors (Winberg 1956; Warren and Davis 1967; Warren 1971; Wiegert 1976). This paper presents data that make up the basic parameters of an energy budget. The basic relation of these components can be presented in:

$$Q_I = Q_W + Q_G + Q_M$$

where Q_I = input energies, whether endogenous, exogenous, or a combination of the two
Q_W = waste energy
Q_G = growth energy
Q_M = metabolic energy.

All but Q_W have been studied by us, and the effects of food density and initial egg size have been discussed. In Figure 9 we present a graphic model of the energy budget of striped bass embryos and larvae fed the high ration diet (5.0 *Artemia*/ml). This model approximates that of Laurence (1977) except that we include input energies of yolk and oil, and we present the relations against time as rates (i.e., calories consumed or expended per 24 h period per organism).

When the energy budget is presented in these terms, some distinctive patterns emerge. Yolk provides a constant energy input until it is exhausted on or about D-7. Oil is used rapidly at first, then more slowly until yolk energy is no longer available and the animal initiates feeding. At this time, the larva increases its use of oil

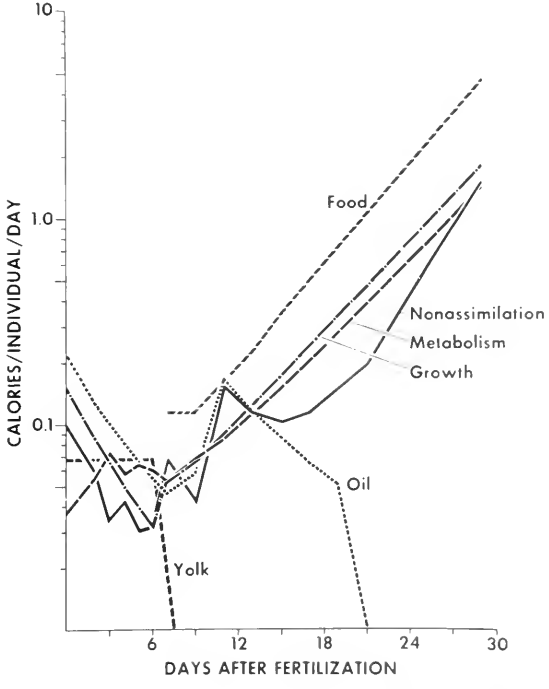

FIGURE 9.—Energy budget of input calories (yolk, oil, and food) and output calories (growth, metabolism, and nonassimilation) presented in calories per individual embryo or larva per day.

until exogenous feeding becomes established, after which it gradually decreases consumption of oil until oil energy is depleted. An initial adjustment to exogenous energy intake is followed by a continuously increasing exogenous input concomitant with decreased reliance on oil energy. Growth showed an interesting pattern that suggested it is closely linked to oil energy prior to feeding and to exogenous food energy after initiation of feeding. Growth rates declined steadily to D-6 and increased abruptly thereafter.

Metabolism increased steadily during incubation and hatching. After the energy consuming hatching process it decreased slightly to the onset of feeding. After D-7, increasing activity associated with feeding resulted in continuously increasing metabolism.

Nonassimilation is the energy remaining after metabolism and growth are subtracted from the total energy input. When energy input is endogenous, nonassimilation comprises poor utilization and/or redeposition of yolk and oil into other tissues. Nonassimilation of exogenous food is mostly due to undigested food. In this model nonassimilation fluctuated with oil input energy and growth to first feeding. It increased during adjustment to feeding and declined when both oil and food calories were available. As *Artemia* became the main energy source nonassimilation increased. Poor digestion in older larvae in the form of nearly intact *Artemia* in the intestines was seen commonly, especially in the high food rations.

The bioenergetics model and its parameters are presently being used to measure various abiotic and biotic stresses, including pollutants. It promises to be a useful method for assessing the effects of these factors.

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STOCK AND RECRUITMENT RELATIONSHIPS IN *PANULIRUS CYGNUS*,[1] THE COMMERCIAL ROCK (SPINY) LOBSTER OF WESTERN AUSTRALIA

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ABSTRACT

Abundance of the breeding stock, level of settlement of the puerulus stage, juvenile densities, and recruits to the fishery for *Panulirus cygnus* from 1969 to 1979 are examined.

A dome-shaped relationship between the index of abundance of the breeding stock and subsequent puerulus settlement indicates that stock-dependent effects during the planktonic larval stages apparently control the level of puerulus settlement. However, density-dependent relationships (characterized by more asymptotic relationships between the various life history stages) dominate after settlement of the puerulus on the coastal reefs and control the level of recruitment to the fishery and eventually to the breeding stock. The relationship between the settlement of the puerulus stage and the catch rates of the recruits entering the fishery 4 years later is adequately described by a Ricker's stock-recruitment curve as is the level of puerulus settlement to the subsequent abundance of the breeding stock. The relationship between the level of puerulus settlement and the later abundance of juveniles at various ages is not clear and possible reasons for this are suggested.

The significance of the stock-dependent relationship between breeding stock and puerulus and the density-dependent relationship between puerulus and breeding stock in maintaining recruitment to the fishery is discussed.

The importance of understanding the stock-recruitment relationship in exploited fish populations has been recognized for many years and has been the subject of several workshops and symposia (e.g., Parrish 1973), as well as a great deal of research. While the importance of such relationships in exploited invertebrate stocks has been equally recognized, quantitative data, particularly for crustaceans, has been virtually nonexistent (Hancock 1973).

Like many fish species, crustaceans in general and spiny (rock) lobsters in particular, pass through several distinct stages in their life history and, as Hancock (1973) pointed out, a proper understanding of the overall stock-recruitment relationship can be gained only by considering the relationship between successive stages over a number of years. Hancock's belief is reinforced by the studies of Larkin et al. (1964) and Paulik (1973) who, having considered the theoretical forms of a stock-recruitment relationship involving such multistage life histories, showed that several stable equilibrium points can exist in the overall spawning stock-recruitment curve, depending on the relationships existing between the various life history stages.

The western rock lobster, *Panulirus cygnus* George, the object of an important fishery in Western Australia (Morgan and Barker 1979) passes through several major stages during its life history. These include a series of phyllosoma larvae, a puerulus stage, and juvenile and adult stages. After a planktonic life of 9-11 mo (Chittleborough and Thomas 1969; Phillips et al. 1979), the surviving phyllosoma larvae metamorphose into a puerulus stage and settle between September and January each year in shallow coastal areas. The younger juveniles concentrate on shallow limestone reefs to depths of 10 m, with some larger juveniles to 20 m. At about 4 or 5 yr of age (i.e., 4 or 5 yr from hatching) juveniles migrate from the shallow reef areas onto the continental shelf into depths of 30-150 m where maturity is reached, mating takes place, and the life cycle is completed.

Chittleborough and Phillips (1975) reported that, based on the data available at that time, indices of year-class strengths obtained from the

[1]The western rock lobster is referred to as *P. longipes* or *P. longipes cygnus* in some of the literature quoted; these are synonymous with *P. cygnus*.

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puerulus at settlement and those derived from measurements of density of juveniles of *P. cygnus* aged 2 or 3 yr were consistent. However, they found survival to recruitment into the fishery did not mirror the pattern of year-class strength at or soon after settlement. The purpose of this paper is to examine the changes that take place in the abundance of the various stages in the life history of *P. cygnus* including data on puerulus settlement and juvenile density and to investigate their interrelationships.

METHODS

The abundance of the several stages in the life history of *P. cygnus* has been measured by various methods over a number of years. The methods used have reflected the practical problems of sampling the different stages and have included catch and fishing effort data from the commercial fishery for the adult stage, collectors composed of artificial seaweed to catch the puerulus stage, and mark and recapture studies of the juveniles using baited traps. All ages and year classes referred to in this paper relate to the year of hatching and so include the 9-11 mo larval phase. For example, the 1969 year class was hatched in January-February 1969 and settled as puerulus larvae between September 1969 and January 1970.

Abundance of the Breeding Stock

The western rock lobster is confined to the western coast of Australia from approximately North West Cape to Cape Naturaliste (Fig. 1). The majority of the commercial catch is taken between lat. 28° and 32°S (Sheard 1962). The coastal fishery operates from 15 November to 30 June of the following year although prior to 1978 the coastal season concluded on 14 August each year. The Abrolhos Islands fishing season which extended from 15 March to 14 August prior to 1978, now also ends on 30 June.

The abundance of the breeding stock (i.e., those females carrying external eggs) has been measured since 1966 from research logbook data supplied on a voluntary basis from about 200 boats or 25% of the commercial rock lobster fleet. In addition to catch, fishing effort, and fishing locality information separated into four depth categories, i.e., 0-10, 10-20, 20-30, and over 30 fathoms, each fisherman records his daily catch of numbers of spawning female rock lobsters.

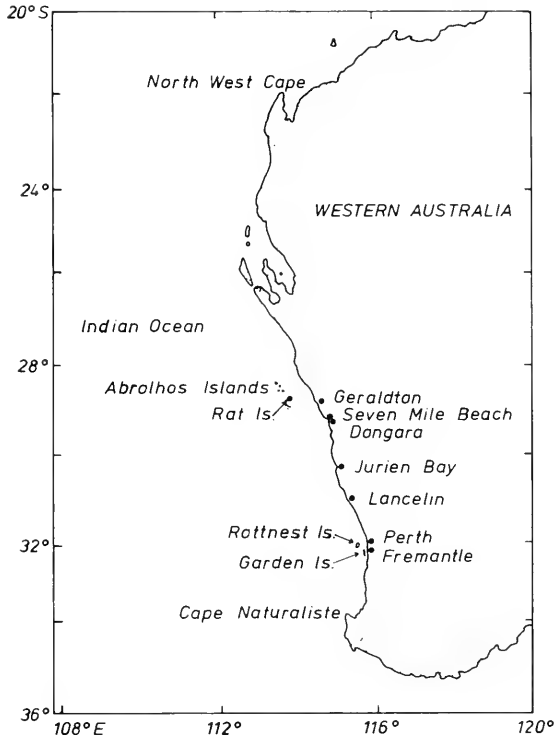

FIGURE 1.—Location of the sites mentioned in the text.

However, these data are not available from the Abrolhos Islands for December, January, and February since this area is closed to commercial fishing at this time each year. Consequently, comparable data on the breeding stock had to be obtained from research vessel cruises to each of the four island groups of the Abrolhos during January and February 1979. Sixty commercial wire beehive pots without escape gaps were set each day for a total of 20 d on the fishing grounds where the greatest concentration of spawning females is to be found. The pots had previously been calibrated in the Garden Island area (Fig. 1) by comparison with commercial catch rates of spawning females. During the comparison, catch rates of spawning females were low (mean of 0.05 animals/pot) and the variances relatively large so it is not surprising that no significant difference (at the 5% level) could be detected between the catch per pot lift of spawning females by the research vessel's pots and the catch per pot lift of spawning females by commercial fishermen's pots. However, additional calibration of the research vessel's pots would add confidence to this conclusion.

Abundance of the Puerulus Stage

Phillips (1972) showed that the last larval stage, the puerulus, of *P. cygnus* could be captured using collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Subsequent studies by Phillips and Hall (1978) have shown that the catches from these collectors provide a measure of the relative strength of settlement from year to year.

All collectors used in this study were as described by Phillips (1972). The collectors were checked monthly after each new moon period when most puerulus settled. All settlement took place at the puerulus stage. The western rock lobsters were removed from the collectors either as puerulus or after they had molted into very small postpuerulus juveniles. Since the planktonic period is 9-11 mo, settlement occurs between September of the year of hatching and the following January.

Abundance of Juveniles

Density of age groups (ages 2-7 yr) has been measured on shallow test reefs at Garden Island (since 1965) and Seven Mile Beach (since 1970), using the single census trap-mark-recapture method described by Chittleborough (1970). These test reefs are adjacent to the collectors used to catch the puerulus stage.

Abundance of Recruits to the Fishery

During late November of each year, large numbers of immature, newly molted, pale colored rock lobsters migrate into deeper water from the shallow water inshore reefs (which are generally inaccessible to fishermen) where they have spent the previous 4 or 5 yr. This offshore movement normally lasts through December and in all lasts about 6 wk. Since they are newly molted, their food requirements are high (Chittleborough 1975) and consequently their catchability by baited pots is high (Morgan 1974). During this migration the fishermen catch large quantities of these animals which are locally known as the "whites" (George 1958). Although a small number of animals undergo two or perhaps three "white" phases in their life cycle, the "white" phase generally occurs only once during an individual's lifetime (George 1958), and this enables the migrating "whites" to be equated with the recruits to the fishery.

Estimates of the abundance of the potential emigrants from the shallow reefs have been made by Chittleborough (1970), although a better measure of their abundance is available from the catch rate (measured as the catch per pot lift) of the commercial fishery during November and December when practically all of the commercial catch consists of "white" rock lobsters. Information on catch and fishing effort for November and December each year has been taken from the fishermen's monthly returns, which are completed as a condition of the fishing license by all fishermen.

RESULTS

Since there have been several customs adopted in the designation of year classes in *P. cygnus* (e.g., Chittleborough 1970; Morgan 1977) a summary of the convention used in this paper will enable the various relationships presented below to be followed more easily. The convention used and the major events in the life history of *P. cygnus* are as follows:

Hatching of eggs	November, December year $x-1$, January, February, and March year x, with midpoint taken as 1 January of year x.
Settlement of puerulus larvae	September year x to January year $x+1$.
Juveniles on inshore reefs	Year $x+1$ to $x+4$ and $x+5$ (ages 1 to 4 or 5).
Migration of "whites" to offshore areas	November and December year $x+4$ and $x+5$, with the majority being $x+4$.
Maturity and first breeding	January and February year $x+6$ and $x+7$, with the majority being $x+6$.

Stock Definition

Based on similarities in catch rates from the commercial fishery, Morgan (1977) concluded that although some population parameters such as growth rates, size at first maturity, etc. varied between localities, the western rock lobster could, as a first approximation, be considered as a single, genetically coherent, unit stock. This view is reinforced by the studies of Phillips et al. (1979) who demonstrated the wide dispersal of

the phyllosoma larvae in the eastern Indian Ocean. Consequently, in the following analyses a single stock has been assumed, although latitudinal differences in some population parameters have necessitated a simple division of the fishery into areas north of lat. 30°S and south of lat. 30°S.

The Breeding Stock

From the research logbook information, it was evident that spawning rock lobsters were concentrated in the 20-30 fathom depth range with an average of 89.9% of the total catch of spawning females each year being taken in this depth range during the period 1966-80. Year-to-year variation was small with the percentage ranging from 86.4% in 1971 to 92.1% in 1967. In addition, the majority of spawning female rock lobsters (average of 81.4% for the period 1966-79) were captured during January and February each year with, again, little year-to-year variation. Accordingly, the catch per pot lift of spawning females taken in 20-30 fathoms in January and February each year has been used as a basis for the calculation of an index of abundance of spawning females. No adjustment for soak time was made since catch per pot lift has been shown to be independent of soak time (Morgan 1977). The use of catch per pot lift data as an index of abundance assumes, of course, that catchability remains constant from year to year. Morgan (1974) has shown that catchability varies during a year in response to molt condition, water temperature, and water salinity. Year-to-year variation in catchability of spawning *P. cygnus* females for January and February is likely to be small, since it would be expected that these animals would be in an intermolt condition, and year-to-year temperature and salinity variation on the spawning grounds in January and February is small (Morgan and Barker 1979).

The average size of the spawning females varies with locality, being larger in southern areas (Morgan and Barker 1979). Average size information on spawning females has been collected on a regular basis since the 1971-72 season from commercial vessels fishing out of the ports of Dongara, Jurien Bay, Lancelin, and Fremantle (Fig. 1). These data have been previously presented in a series of annual reports on the fishery (e.g., Morgan and Barker 1979). Occasional collections of size composition data of spawning females were made prior to the 1971-72 season, particularly at Jurien Bay and Lancelin (B. K. Bowen, unpubl. data). These two sources of data have been used to calculate the average size of spawning female *P. cygnus* for various years. The relationship between size and fecundity (Morgan 1972) has then been used to calculate the number of eggs produced by a spawning female rock lobster of this average size. *Panulirus cygnus* spawns only once per year in most areas in the wild (Morgan 1980b).

Data on the catch rates of spawning female *P. cygnus* taken in 20-30 fathoms in January and February each year, the mean size of these spawning females, and the resultant fecundity are shown in Table 1, separated into two areas: north of lat. 30°S and south of lat. 30°S.

Index of Abundance of Spawning Stock

The most appropriate index of spawning success in *P. cygnus* is the number of first stage phyllosoma larvae released during the hatching period. However, since it has not been possible to measure phyllosoma abundance directly, an indirect measure, utilizing the abundance and fecundity of the spawning females, is necessary. Thus the total number of first stage phyllosoma larvae released is approximately equal to (total number of spawning females) × (their average fecundity).

The number of spawning females in each of the two coastal areas (north and south of lat. 30°S) may be estimated from their catch rate (a measure of density) multiplied by the area of the spawning grounds. The area of the spawning grounds for coastal localities north and south of lat. 30°S is given in Table 2. Thus, for example, a measure of the total number of spawning females north of lat. 30°S in 1966 is given by 0.44 (from Table 1) × 6,690 (from Table 2) = 2,943.6. It should be noted that this measure gives a relative, not an absolute, figure for the numbers of spawning females since a knowledge of the catchability coefficient per unit area, q, would be necessary to convert catch rate (c/g) into absolute numbers (N) by using the relationship

$$c/g = \frac{q \times N}{A}$$

where A = area of the spawning grounds.

Catchability has been measured at the Abrol-

TABLE 1.—Catch (numbers) per pot lift of spawning female *Panulirus cygnus* taken in 20-30 fathoms in January and February each year (c/g), the mean size of the spawning females (S) (in millimeters carapace length), and the resultant fecundity at this size (F), for two coastal areas. The method of calculation of the index of abundance of the breeding stock (I.A.S.) is explained in the text. NA = Not yet available.

	Coastal areas north of lat. 30°S			Coastal areas south of lat. 30°S			All coastal areas	All coastal and Abrolhos areas
Year	c/g	S (mm CL)	F	c/g	S (mm CL)	F	I.A.S. ($\times 10^7$)	I.A.S. ($\times 10^7$)
1966	0.44			0.53			174	198
1967	0.61	92.2	321,710	0.33			179	204
1968	0.50	90.2	302,110	0.65			205	234
1969	0.49			0.28			146	166
1970	0.40			0.34			136	155
1971	0.23			0.23			84	96
1972	0.48	92.9	328,570	0.16	104.3	440,290	125	143
1973	0.22	90.5	305,050	0.15	104.6	443,230	69	79
1974	0.12	91.3	312,890	0.08	106.4	460,870	37	42
1975	0.14	94.5	344,250	0.13	105.0	447,150	49	56
1976	0.16	93.5	334,450	0.13	104.0	437,350	54	62
1977	0.24	92.0	319,750	0.16	103.9	436,370	75	86
1978	0.24	92.8	327,850	0.11	104.6	443,230	67	76
1979	0.27	NA		0.17	NA		83	95
1980	0.19	NA		0.11	NA		56	64

TABLE 2.—Comparison of egg production estimates for coastal areas north and south of lat. 30°S and the Abrolhos Islands area for 1979.

	Abrolhos	North of lat. 30°S	South of lat. 30°S	Total
Area of spawning grounds from Admiralty charts (km^2) (A)	840	6,690	3,500	11,030
Average size of spawners (mm carapace length (B))	74 (research cruise data)	94 (Morgan and Barker 1979)	105 (Morgan and Barker 1979)	
Fecundity (from Morgan 1972) (C)	143,300	339,300	447,150	
Catch per pot lift of spawning females (D)	1.16 (from research vessel)	0.27 (from fishermen's log books)	0.17 (from fishermen's log books)	
Relative numbers A × D (E)	974	1,906	595	
Egg production $\times 10^7$, E × C (F)	13.99	61.29	26.60	101.88
Percentage egg production	14%	60%	26%	100%

hos Islands (Morgan 1974) but it has not been considered necessary to introduce additional assumptions by converting relative to absolute numbers. From Table 1, it is apparent that for each area the average size of spawning female *P. cygnus* has remained approximately constant for the years for which data are available, although significant differences are apparent between the two coastal areas. Consequently, the mean value of the yearly average sizes for each area has been taken and used to calculate average fecundity for the years 1966-80 using the relationship given by Morgan (1972). These values are north of lat. 30°S, $\overline{CL}$ 92 mm (fecundity 319,750) and south of lat. 30°S, $\overline{CL}$ 105 mm (fecundity 447,150). Calculation of an index of abundance of the spawning stock for each coastal area each year can now be made while summation for each year gives the index for all coastal areas. These are as follows:

North of lat. 30°S: Catch rate × 6,690 × 319,750.
South of lat. 30°S: Catch rate × 3,500 × 447,150.
All coastal areas: Catch rate (north of lat. 30°S) × 6,690 × 319,750 + catch rate (south of lat. 30°S) × 3,500 × 447,150.

Annual indices of abundance of the spawning stock for all coastal areas are shown in Table 1. It should be noted that this is a more refined index than that used by Morgan (1980a).

During the research vessel cruises in the Abrolhos Islands area in January and February 1979, the average catch per pot lift of spawning females was 1.16 or about six times that of coastal areas. However, as shown in Table 2, the small geographical area and the smaller average size of spawning female *P. cygnus* reduces the apparent importance of the Abrolhos Islands area, both in terms of the number of spawning females

and their egg production, when compared with the coastal areas.

The Abrolhos Islands area, therefore, contributed only about 14% of total egg production in 1979. No data on the catch rates of spawning females at the Abrolhos Islands are available for years other than 1979, so it has had to be assumed that the Abrolhos Islands area contributed 14% of the total egg production in each year from 1966, although year-to-year variation in the geographical distribution of settling puerulus larvae will no doubt change this value to some extent. The index of abundance of the spawning stock for all coastal and Abrolhos Islands areas has therefore been estimated by multiplying the coastal index for each year by 1.14. These values are also shown in Table 1.

Abundance of Puerulus Stage

The relative densities of settlement of the puerulus stage (expressed as the mean number per collector settling between September and January at Rat Island (Abrolhos Islands), Seven Mile Beach, Jurien Bay, and Garden Island) are given in Table 3. The data for the different sites have been pooled as an unweighted arithmetic mean and expressed as the mean number of puerulus settling on the collectors, to provide an annual index of settlement.

Abundance of Juveniles

Estimated densities of various year classes at Garden Island and Seven Mile Beach were calculated as described by Chittleborough and Phillips (1975) (Table 4).

Abundance of Recruits to the Fishery

The catch per pot lift of "white" rock lobsters taken during November and December has varied during the years 1964-78 (Table 5) and has resulted in similar variations in total catch from the fishery (Table 6).

The Relationships

Spawning Stock and Puerulus Settlement

Since the peak of puerulus settlement each year occurs from September to January (Phillips and Hall 1978) and is the result of spawning in the previous January and February (Chittleborough and Phillips 1975), the settlement of puerus-

TABLE 3.—Mean number of puerulus settling per collector. — = not measured.

Year of hatching	Index annual settlement	Rat Island	SE	Seven Mile Beach	SE	Jurien Bay	SE	Garden Island	SE
1969	9.7	—		15.2	1.90	4.2	1.07	—	
1970	22.4	[1]35.8	8.94	35.0	2.72	17.8	5.00	0.8	0.85
1971	38.8	47.5	3.12	67.3	5.00	34.7	4.50	2.5	1.90
1972	35.7	68.8	3.90	33.7	3.14	39.6	3.12	0.8	0.85
1973	71.4	73.8	6.07	83.2	4.74	117.4	10.96	11.0	3.06
1974	126.3	130.8	8.83	159.8	12.48	209.6	22.04	5.1	2.55
1975	73.2	105.8	8.60	97.3	6.03	79.6	6.07	10.2	2.25
1976	72.3	106.8	7.09	114.3	7.77	65.6	5.67	2.6	0.81
1977	68.4	112.8	7.85	86.0	7.01	72.2	6.81	2.4	0.60
1978	114.5	182.6	19.33	182.8	11.69	82.4	6.53	10.2	2.59
1979	71.0	102.5	7.42	76.2	4.28	94.4	16.74	11.0	2.67

[1]Converted from two collectors to a different set of four collectors to ensure compatability with later samples.

TABLE 4.—Estimates of year-class strength (no./ha) for juvenile western rock lobsters on nursery reefs (in January). — = not measured; NA = not yet available.

Age (yr)	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
Garden Island																
2	—	3,800	4,400	1,400	500	1,200	700	150	1,500	2,600	404	1,932	1,246	2,381	957	1,340
3	3,245	1,070	3,324	317	265	875	537	92	971	1,200	274	1,053	765	969	630	1,300
4	921	810	730	174	195	685	333	60	448	813	149	646	311	638	611	NA
5	697	178	401	128	152	424	217	28	304	443	91	366	205	618	NA	NA
Seven Mile Beach																
2	—	—	—	—	—	—	6,200	6,100	5,100	12,100	11,767	29,869	9,952	5,449	40,163	29,503
3	—	—	—	—	—	5,779	3,825	2,318	2,135	7,591	5,460	4,316	5,012	2,828	6,145	4,986
4	—	—	—	—	—	3,540	1,461	978	1,339	3,522	789	2,174	2,598	433	1,039	NA
5	—	—	—	—	—	1,352	616	613	621	509	397	1,127	397	73	NA	NA

TABLE 5.—Catch (kg) per pot lift of rock lobsters taken by the commercial fishery during November and December for the years 1964-79.

Year	Catch (kg)/pot lift	Year	Catch (kg)/pot lift
1964	1.300	1972	1.057
1965	1.344	1973	0.674
1966	1.352	1974	0.997
1967	1.713	1975	1.115
1968	1.304	1976	1.079
1969	0.973	1977	1.238
1970	1.001	1978	1.443
1971	1.029	1979	1.364

TABLE 6.—Total catch for the western rock lobster fishery.

Season	Total catch (kg $\times 10^6$)	Season	Total catch (kg $\times 10^6$)
1965-66	8.120	1973-74	6.780
1966-67	8.635	1974-75	8.877
1967-68	9.853	1975-76	8.731
1968-69	8.078	1976-77	9.281
1969-70	6.918	1977-78	10.742
1970-71	8.013	1978-79	11.429
1971-72	8.171	1979-80	10.698
1972-73	6.809		

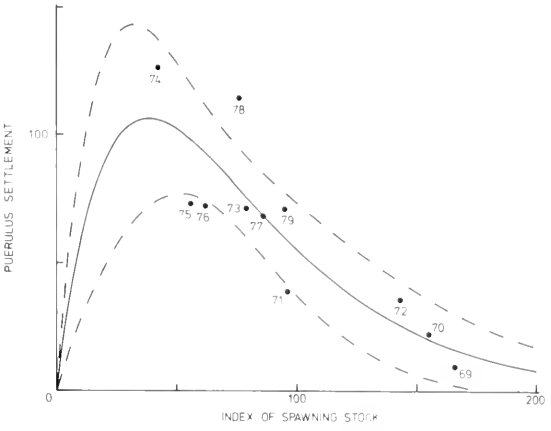

FIGURE 2.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of abundance of spawning *Panulirus cygnus* and the resultant level of settlement of the puerulus stage. The year shown is the season of hatching of the larvae.

lus in year x (plus January of year $x+1$) may be compared directly with the index of abundance of the spawning stock (I.A.S.) in year x.

The Ricker (1958) stock-recruitment relationship of $R = AS\ \exp(-BS)$, where R = recruitment, S = stock size, A = coefficient of density-dependent survival, and B = coefficient of density-independent mortality, was fitted using the method of Cushing and Harris (1973). The relationship is shown in Figure 2 and provides a good fit to the observed data (proportion of sum of squares explained is 0.775). Estimates of A and B with their standard errors (SE) are $A = 7.645$, SE = 2.193 and $B = 0.026$, SE = 0.004.

Puerulus and Juvenile Densities

The relationship between puerulus and juvenile densities is not clear. In contrast to the statement of Chittleborough and Phillips (1975) that puerulus settlement is a good indicator of subsequent juvenile density, the additional data available for Seven Mile Beach (Table 7) indicate that the correlation between puerulus settlement and the subsequent density of 2-yr-old juveniles is poor ($r = 0.359$, $P > 0.05$). Neither do the data give an acceptable fit to a Ricker (1958) stock-recruitment curve. The same conclusion is reached from examination of Garden Island data (Tables 3, 4) ($r = 0.528$, $P > 0.05$). For example, relatively high settlement of puerulus at Seven Mile Beach in 1974 and 1977 (Table 7) when total juvenile density was also high gave rise to very poor and very high densities, respectively, of 2-yr-olds. Beyond 2 yr of age, however, density-dependent mortality is evident. At both Garden Island and Seven Mile Beach there was a significant ($P < 0.001$)

TABLE 7.—Level of puerulus and subsequent juvenile densities of *Panulirus cygnus* in January and mortality rates at Seven Mile Beach, Western Australia. — = not measured; NA = not yet available; arrows connect individual year classes.

Year of hatching	Puerulus mean no settling/ collector	Age in years of juveniles arising from puerulus				Juveniles present on reef at time of puerulus settlement	Mortality rate/yr of animals aged ≥ 3 yr
		2 No./ha	3 No./ha	4 No./ha	5 No./ha	Total no./ha 2-5 yr	
1969	15.2	6,200	—	—	—	—	—
1970	35.0	6,100	3,825	3,540	—	—	—
1971	67.3	5,100	2,318	1,461	1,352	10,231	0.863
1972	33.7	12,100	2,135	978	616	15,829	0.466
1973	83.2	11,767	7,591	1,339	613	21,310	0.768
1974	159.8	29,869	5,460	3,552	621	39,472	1.934
1975	97.3	9,952	4,316	789	509	15,566	0.686
1976	114.3	5,449	5,012	2,174	397	13,032	0.657
1977	86.0	40,163	2,828	2,598	1,127	46,716	1.879
1978	182.8	29,503	6,145	433	397	36,478	1.780
1979	76.2	NA	4,986	1,039	73	NA	NA

correlation between total density of juveniles on the test reefs and annual mortality rate.

Puerulus Settlement/Juvenile Densities and Recruitment to the Fishery

Chittleborough and Phillips (1975) examined the relationship between the density of larger juveniles on the coastal reefs during the latter part of the year and the success of the commercial white fishery in adjacent waters. They found that, although density-dependent mortality during the juvenile phase ensures reasonably constant recruitment to the fishery over a wide range of initial year-class strengths, in some years the level of puerulus settlement may be inadequate (i.e., below the holding capacity of the shallow-water reefs), and poor recruitment to the fishery may result. They reported that from the data available at that time only the incidence of particularly poor year classes could be used to predict the relative success of the "white" fishery, i.e., to forecast poor future recruitment to the fishery.

Thus, as reported by Hancock (1971), following the low settlement of puerulus larvae on the collectors in 1969-70 (the hatchings of January-March 1969) and low density of early juveniles, it was predicted by Chittleborough and Phillips in 1971 (Anonymous 1974) that low catch levels would be likely in 1972-73 and even lower levels likely at the opening of the 1973-74 season (i.e., the "whites" of November and December 1973). This prediction was borne out by the catches of these 2 years (Anonymous 1974), the white season of 1973 being the poorest on record, particularly in the Fremantle area (reflecting trends observed in the Garden Island research area).

It was pointed out by Chittleborough and Phillips (1975) that the appearance of a very strong settlement, such as that resulting from the hatchings of 1974 at Seven Mile Beach, did not necessarily mean that a high level of recruitment to the fishery could be predicted for the 1977-78 and 1978-79 seasons. The preceding year classes were relatively strong so that the year class of 1974 faced intense competition and high mortality while on the "nursery" reefs. Nevertheless, the 1978 "white" catch rate was the second highest on record.

Figure 3 shows that in fact a good relationship does exist between the level of settlement of the puerulus and the subsequent catch rate (measured as the catch per pot lift) of the "whites" 4 yr later. (Proportion of sum of squares accounted for is 0.574.) The relationship is well described by a Ricker (1958) stock-recruitment curve, fitted by the method of Cushing and Harris (1973). Parameter estimates and their standard errors (SE) are $A = 0.048$, SE $= 0.0066$ and $B = 0.012$, SE $= 0.0018$. A similarly good relationship is achieved by using the puerulus settlement data from Seven Mile Beach only; this is to be expected because of their close correlation with the annual index of settlement ($r = 0.966$, $P<0.01$).

Since the "whites" catch contributes about 40% of the total catch of any one season, it follows from Figure 3 that there should also be a good relationship between the level of puerulus settlement in year x and the total commercial catch rate of the season beginning in November, year $x + 4$, despite the inevitable confusion of year classes in catches taken after December (i.e., after the "whites") each season. The total commercial catches for 1965-66 to 1978-79 are shown in Table 6. The influence of the poor white catch rate of 1973 and the high white catch rate of 1978 on total catches of these years can be clearly seen.

Puerulus Settlement and Subsequent Spawning Stock

Whereas the relationships between the other stages in the life history of *P. cygnus* are not influenced by the effects of fishing mortality, the rela-

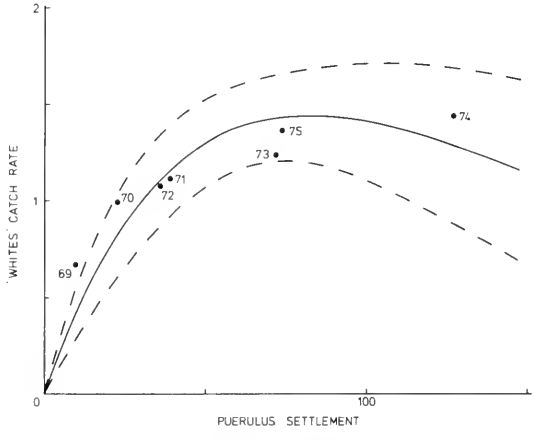

FIGURE 3.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent catch rates of *Panulirus cygnus* at recruitment into the fishery 4 yr later. The year shown is the season of hatching of the larvae.

tionship between puerulus settlement and the subsequent spawning stock will inevitably be confused by the effects of variable amounts of fishing pressure on the commercial stocks between the time the rock lobsters are recruited to the fishery as whites and the time that they become mature. In addition, the mature females will be subjected to fishing pressure when they are not carrying eggs. When they are carrying eggs, the fishermen are required by law to return these mature females to the sea.

This fishing pressure on the mature and immature stocks will lead to a reduction in the abundance of the spawning females compared with their potential abundance if there was no fishing pressure. Moreover, the degree of reduction will be a function of the fishing effort (f) since

$$N_t = N_0 e^{-(M+qf)t}$$

where N_t = numbers present at time t
N_0 = numbers present at time 0
M = instantaneous natural mortality rate
q = catchability coefficient.

If the growth rate of *P. cygnus* is considered (Morgan 1977), it will take approximately 1 yr in coastal areas north of lat. 30°S for female rock lobsters to grow from the legal minimum length of 76 mm to the average size of a mature female of 92 mm (Table 1) and approximately 2 yr in areas south of lat. 30°S to grow from 76 mm to the average size of a mature female of 105 mm. Therefore, as a first approximation and neglecting the apparently small influence of the Abrolhos Islands area, it will be assumed that female *P. cygnus* are subjected to fishing pressure for an average of 1.5 yr during their life in the fishery. The indices of abundance of the spawning stock for all areas (Table 1) can now be adjusted to take into account the probable effects of fishing pressure by assuming the index for any year, i, is not only a result of puerulus settlement in previous years but has been reduced by the effect of fishing effort in year $(i-1)$ and one-half the fishing effort in year $(i-2)$.

Using the effective fishing effort data given by Morgan (1979) and Hancock (1981), a relative index, R.I., for later years can be calculated so that it takes into account the effects of fishing effort prior to maturity. This will be given by

$$\text{R.I.}\ (i) = \text{I.A.S.}(i)/\exp\left(-q(f(i-1) + 0.5\, f(i-2))\right)$$

where $f(i-1)$ = fishing effort in year $i-1$
$f(i-2)$ = fishing effort in year $i-2$
I.A.S.(i) = index of abundance of the breeding stock in year i.

Using the values of fishing mortality rate F and effective effort, f, given by Morgan (1977) a value of q may be calculated from

$$q = \frac{F}{f}.$$

This gives an average value of q for the period 1967-73 of 1.4×10^{-7}.

Using the above formula and value of q, relative indices of abundance have been calculated and are shown in Table 8.

The spawning stock will inevitably comprise a number of year classes each of which is the result of puerulus settlement some 6 yr earlier. However, at the high levels of fishing effort which have been characteristic of the fishery in recent years (Morgan 1979) the breeding stock will be dominated by the younger year classes. Using the value of q of 1.4×10^{-7} and the value of the natural mortality rate M of 0.226 (Morgan 1977), it can readily be shown that during the 1978-79 season, the total instantaneous mortality rate Z was about 1.54. At this level of mortality, only about 21% of spawning females may be expected to survive for a second year's spawning and about 5% for a third year.

The relative indices of the spawning stock

TABLE 8.—The relative index of the breeding stock (R.I.) calculated from the index of abundance of the breeding stock (I.A.S.), and adjusted for fishing effort. The method of calculation is explained in the text. NA = not yet available.

Fishing season	I.A.S. ($\times 10^7$) from Table 1	Fishing effort ($\times 10^6$)	R.I. ($\times 10^7$)
1963-64		4.798 (assumed)	
1964-65		4.798	
1965-66	198	5.036	542
1966-67	204	5.147	578
1967-68	234	5.173	684
1968-69	166	4.292	491
1969-70	155	5.771	406
1970-71	96	7.888	291
1971-72	143	7.536	646
1972-73	79	7.253	394
1973-74	42	7.127	196
1974-75	56	8.035	252
1975-76	62	8.100	314
1976-77	86	8.339	469
1977-78	76	9.765	431
1978-79	95	9.357	668
1979-80	64	NA	470

shown in Table 8 will therefore represent a majority of 6-yr-old spawning females with relatively minor contributions from older year classes. The relative index (R.I.) of the spawning stock may then be directly related to the puerulus settlement 6 yr earlier. This relationship is shown in Figure 4 where again, a Ricker (1958) stock-recruitment relationship provides a good description of the data. (Proportion of sum of squares accounted for is 0.845.) Parameter estimates and their standard errors (SE) are $A = 21.17$, SE $= 2.43$ and $B = 0.013$, SE $= 0.0016$. This relationship however may be less apparent at lower levels of fishing effort where the spawning stock would not be so dominated by the younger year classes.

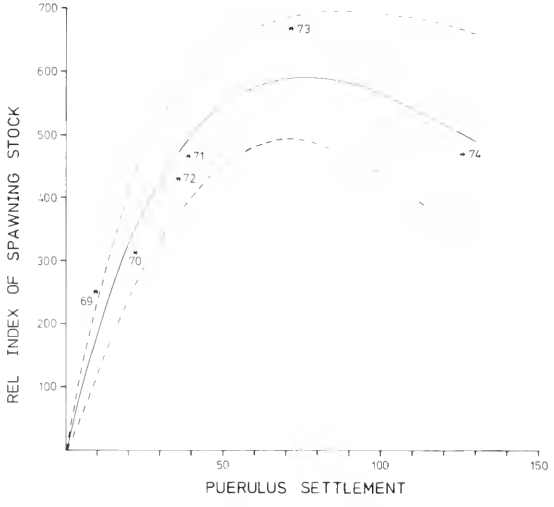

FIGURE 4.—The Ricker (1958) stock-recruitment model, together with 95% confidence limits. The model is fitted to data on the index of the annual level of puerulus settlement and subsequent relative abundance of the breeding stock (i.e., adjusted to the same level of fishing effort as explained in the text) of *Panulirus cygnus*. The year shown is the season of hatching of the larvae.

DISCUSSION

During the period 1969-79, it has been possible to measure abundance of the various life history stages of the rock lobster *P. cygnus* using a variety of methods. The subsequent preliminary analysis of the interrelationships, shown in Figures 2-4 and Table 7, has provided information both on the regulatory strategies of the *P. cygnus* population and on the effect of fishing pressure on the stocks.

A dome-shaped relationship is apparent in Figure 2 which is indicative of strong stock-dependent effects (following the terminology of Harris 1975) operating during the planktonic larval stages of *P. cygnus*. This results in the greatest abundance of puerulus being produced by an initially small number of spawning females and a very much lower abundance of puerulus being produced by a large number of spawning females. Cushing (1971) and Cushing and Harris (1973) have shown that such dome-shaped relationships are characteristic of fish with high fecundities, whereas those with low fecundities have more asymptotic relationships. In this respect, the western rock lobster is highly fecund (Morgan 1972), a characteristic which confers upon the species a greater capacity for stabilization and resistance to environmental perturbations. The mechanism by which this stock-dependent mortality occurs is not known, although Harris (1975) and Cushing and Horwood (1977) have shown that such pronounced dome-shaped stock-recruitment relationships can only occur when the number of predators (or cannibals) is explicitly related to the number of eggs or larvae released. Chittleborough (1979) suggested that low levels of zooplankton off the west coast of Australia impose density-dependent (stock-dependent in Harris terminology) mortality upon *P. cygnus* larvae.

Once the puerulus have settled in the coastal reef systems, more asymptotic relationships are apparent which are indicative of density-dependent, rather than stock-dependent, processes (Harris 1975). This results in more asymptotic relationships between the level of puerulus settlement and the subsequent abundance of recruits to the fishery (Fig. 3) and to the breeding stock (Fig. 4). The intermediate relationship between the level of puerulus settlement and the abundance of juveniles of various ages (Table 7) does not appear to be as clear. This may be a result of the juvenile abundance being measured on small areas of reef which may, or may not, be representative of the abundance of juveniles over a wider area. It is possible, at times of high puerulus settlement, that reef areas underutilized or not normally used by juveniles may be occupied. Alternatively the area available to juveniles for either shelter or food supply may vary over a period of years because of changing reef siltation or seagrass bed development. Dramatic changes in reef occupancy by juvenile and adult *Panulirus homarus homarus* (Linnaeus) caused by siltation have been observed at Durban in South

Africa by Smale (1978), and similarly Booth (1979) suggested that varying survival and possible changes in location of juveniles may occur in *Jasus edwardsii* (Hutton) at Castlepoint in New Zealand as a result of periodic sand movement in the area. Chittleborough (1975) has pointed out that the availability of food on the coastal reefs is probably the predominant factor limiting the survival of juveniles. Studies in progress should provide further data to examine this hypothesis. The role of competitors and predators also requires further examination.

Because of the close relationship between the level of puerulus settlement and subsequent abundance of recruits to the fishery, the level of puerulus settlement can be taken as an indicator of the likely level of the future fishery. The data for Seven Mile Beach, which is near the center of the range of population, appears to provide a satisfactory basis for this prediction up to the present time. However, its use as the sole measure of puerulus settlement would introduce assumptions regarding the future puerulus distribution. The densities of juveniles on small test reefs do not appear at this time to provide a good basis for estimation of the future recruitment to the fishery.

The combination of a stock-dependent relationship between breeding stock and puerulus settlement and a density-dependent relationship between puerulus and breeding stock will result in a population which has only one stable equilibrium point of abundance (Paulik 1973), the location of this point being dependent upon the fishing mortality rate on spawning and prespawning animals. If fishing effort is high the number of spawning female rock lobsters will be reduced, which, from Figure 2, will lead to a higher level of puerulus settlement. This higher level of puerulus settlement will then result in a good recruitment of "whites" to the fishery. The possibility of incorporating the relationships between these various life history stages into a production model of the fishery is therefore feasible and warrants further investigation. However since the results presented here are preliminary, in the sense that a longer time series of data would be needed to add confidence to the relationships shown in Figures 2-4, such a production model may at present be premature.

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SPAWNING, AGE DETERMINATION, LONGEVITY, AND MORTALITY OF THE SILVER SEATROUT, *CYNOSCION NOTHUS*, IN THE GULF OF MEXICO[1, 2]

DOUGLAS A. DEVRIES[3] AND MARK E. CHITTENDEN, JR.[4]

ABSTRACT

Cynoscion nothus females from the Gulf of Mexico off Texas matured at 140-170 mm SL as they approached age I. Spawning occurred from early May through late October but primarily in two periods, May and August-September. Greatest spawning occurred in the August-September period when two distinct spawned groups (intrayear class cohorts) were produced. The multiple-spawned group structure within a year class may be important to the population dynamics and stability of *C. nothus*. This species reached 130-190 mm SL at age I. Only one year class occurred or dominated in any one month, and only two year classes were ever present at once. The largest specimen captured was 190 mm SL, and 99% were <160 mm. The maximum life span (t_L) was only 1-1.5 years off Texas but might be 2 years in the northcentral gulf. The total annual mortality rate was best estimated at 99.83% and probably is no lower than 90% if the life span is as long as 2 years. Larger *C. nothus* almost disappeared during winter suggesting an offshore movement for overwintering.

The silver seatrout, *Cynoscion nothus*, smallest of four congeners found along the U.S. Atlantic coast, ranges from Chesapeake Bay to the Bay of Campeche (Hildebrand and Schroeder 1928; Hildebrand 1955). *Cynoscion nothus* is one of the more abundant fishes of the nearshore waters of the northern Gulf of Mexico (Hildebrand 1954; Moore et al. 1970; Gutherz et al. 1975). It is not considered an estuarine species (Ginsburg 1931; Hildebrand and Cable 1934), but small numbers of *C. nothus* have been taken in bays throughout the year (e.g., Gunter 1938, 1945; Swingle 1971; Dahlberg 1972).

Despite its abundance, no published study has been directed at *C. nothus* in the gulf. Little is known about its life history, although Mahood (1974) described spawning and monthly size composition in Georgia waters. General notes on *C. nothus* appear in many faunal studies, including Hildebrand and Cable (1934), Gunter (1938, 1945), Chittenden and McEachran (1976), and in a literature review by Guest and Gunter (1958).

This paper describes age determination for silver seatrout, spawning seasonality and periodicity, growth, mortality, diel changes in availability, and total weight-standard length, girth-standard length, and standard length-total length relationships.

METHODS

Collections were made monthly from February through December 1977 and in March 1978 in the Gulf off Port Aransas, Tex., aboard the Texas Parks and Wildlife Department's RV *Western Gulf*, using a 13.7 m otter trawl with 5.1 cm stretched mesh in the cod end. Stations were usually occupied at 11 m depth at night and at 7, 15, and 18-24 m during the day. Additional night collections were made from May through October 1977 at 20-22, 29-31, and 38 m.

Cynoscion spp. were fixed in 10% Formalin[5] and transferred to 40% isopropanol before processing. *Cynoscion nothus* were separated from *C. arenarius* primarily by comparing the anal fin base to the eye width, a procedure based on the comparatively low anal fin ray counts and larger eye size that Ginsburg (1929) reported in *C. nothus*. The anal fin width equals or is only slightly greater than eye width in *C. nothus*, but

[1]Based on a thesis submitted by the senior author in partial fulfillment of the requirements for the M.S. degree, Texas A&M University.

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

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it is about 1.5-2 times the eye width in *C. arenarius*. Standard length (SL) was measured on all fish captured off Port Aransas. A random number table was used to select 300 specimens each month for intensive processing to determine age, total weight (TW), standard length, girth (G) at the anterior origin of the dorsal fin, sex, gonad weight to the nearest 0.1 g, and gonad maturity stage. All specimens were processed if <300 were collected in any month, and all fish larger than the following sizes were processed: 150 mm SL in April, 75 mm in September, 75 mm in October, 150 mm in November, and 110 mm in December. Maturity stages were assigned to immature and female fish (Table 1) using a slight modification of Kesteven's system (Bagenal and Braum 1971). Scales were taken above the lateral line over the anal fin, where they normally persisted. Cellulose acetate impressions were examined, using a scale projector initially, but a dissecting microscope was employed for a second reading made a year later. No scales were taken from fish <60 mm SL. Annuli were identified knowing the size and collection date of each fish and using standard criteria (Tesch 1971) and procedures used for *C. nebulosus* and *C. regalis* (Klima and Tabb 1959; Tabb 1961; Massman 1963; Merriner 1973). Specific characters used to identify annuli included 1) a definite clear zone between circuli in the anterior field (Fig. 1), 2) appearance of secondary radii *in conjunction with* the clear zone, 3) cutting over of circuli in the lateral field, and 4) appearance of these characters on all or most scales examined. Marks interpreted as false annuli appeared on only a few scales from a fish, usually lacked cutting over, or lacked a clear zone between circuli in conjunction with secondary radii.

Additional specimens were collected monthly from October 1977 through July 1978 off Freeport, Tex., using double-rigged 10.4 m (34 ft) shrimp trawls with 4.4 cm stretched cod end mesh. These collections were made during the day at 7-9, 11, 15-17, 18, 27, 37, and 46 m. Total length (TL) was measured on all fish captured and converted to standard length, using regression relationships presented herein. These length frequencies were used to support findings based on collections off Port Aransas.

Spawned group identities (intrayear class cohorts) within each year class were indicated by specifying the year and probable month when they hatched, e.g., August$_{76}$. Spawning periodicity and group identities assume that a 30 mm TL

TABLE 1.—Description of gonad maturity stages assigned to *C. nothus*.

Stage	Description
Immature	Gonads not visible or barely visible, sexes indistinguishable.
Maturing virgin	Gonads visible but very small, sexes indistinguishable to naked eye.
Early developing	Ovaries small, reddish, occupy 10% or less of body cavity, individual eggs not visible to naked eye.
Late developing	Ovaries orangish yellow, extend length of body cavity and occupy 25-50% of it, opaque eggs clearly discernible to naked eye.
Gravid	Ovaries occupy 50% or more of body cavity, up to half the eggs translucent.
Ripe	Ovaries fill over half the body cavity, no fat along inner margins of ovaries, over half the eggs translucent.
Spawning/spent	Ovary flaccid, partially or completely empty, no opaque eggs.
Resting	Ovaries small but distinguishable in fish large enough to be mature.

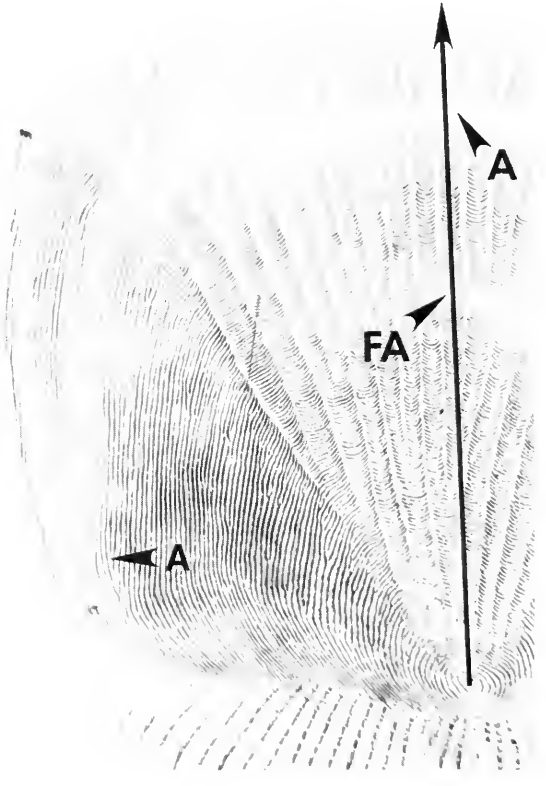

FIGURE 1.—Scale from a 177 mm SL *C. nothus* captured in June showing one annulus (A). The annulus is identified by cutting over in the lateral field and secondary radii in conjunction with a clear zone between circuli. A false annulus (FA) lacks cutting over and was absent on several scales. The axis depicted by the long arrow indicates where scale measurements were made.

(about 21 mm SL) at 1 mo of age for *C. regalis* (Welsh and Breder 1923) can be extrapolated to *C. nothus*. Size descriptions of spawned groups (Table 2) were based upon major portions of specific frequency distributions cited; approximate modes and/or midranges were used to describe central tendency as judged best, often ignoring extreme sizes. Ages when spawned groups disappeared (Table 3) assume hatching at the beginning of months specified in the group identity. Maximum life span was approximated in the sense of the Beverton-Holt model parameter t_L (Gulland 1969) following Alverson and Carney's (1975) definition that only about 0.5-1% of the catch exceeds age t_L or its corresponding lengths.

RESULTS

Spawning

Cynoscion nothus mature at 140-170 mm SL as

TABLE 2.—Growth data for spawned groups of *C. nothus* from the Gulf of Mexico off Port Aransas and Freeport, Tex. Unadjusted growth increments between indicated collection dates were converted to growth/30 d and plotted in Figure 7. Blank spaces in columns for modes and growth increments represent instances in which we consider size data (Figs. 3, 4) too unclear to warrant further analysis.

Spawned group and collection date	Age (mo)	Size range (mm SL)	Mode (M) or midrange (MR) (mm SL)	Unadjusted growth increment (mm SL)
		PORT ARANSAS		
September$_{77}$				
10-11 Nov. 77	2	30-60	47	8
1 Dec. 77	3	40-75	55	
August-September$_{76}$				
9 Feb. 77	5-6	40-75	49 (M)/57 (MR)	8 (M)/8 (MR)
14, 29 Mar. 77	6½-7½	40-90	57 (M)/65 (MR)	7 (M)/8 (MR)
5-6 Apr. 77	7-8	45-100	64 (M)/73 (MR)	30 (MR)
22-26 May 77	9-10	85-120	103 (MR)	20 (MR)
29-30 June 77	10-11	105-140	123 (MR)	27 (MR)
19 July 77	10½-11½	130-170	150 (MR)	
August-September$_{77}$				
8 Mar. 78	6-7	45-115		
May$_{76}$				
5-6 Apr. 77	11	130-160		
22-26 May 77	12½-13	155-170		
7 June 77	13	155-180		
29-30 June 77	14	160-185		
May$_{77}$				
19 July 77	2½	52-61		
2 Aug. 77	3	78		
20-28 Sept. 77	4½	70-115		
5 Oct. 77	5	80-125		
10-11 Nov. 77	6	100-155		
1 Dec. 77	7	115-150		
August$_{77}$				
20-28 Sept. 77	1½	25-70	41 (M)	15
5 Oct. 77	2	35-85	56 (M)	21
10-11 Nov. 77	3	55-100	77 (M)	18
1 Dec. 77	4	75-115	95 (M)	
		FREEPORT		
September$_{77}$				
5 Nov. 77	2	22-55	40 (M)	10
2-3 Dec. 77	3	25-75	50 (M)	
August-September$_{77}$				
19-20 Feb. 78	5½-6½	48-110	79 (MR)	
21-22 Mar. 78	6½-7½	42-112	77 (MR)/42 (L)	13 (MR)/13 (L)
14-15 Apr. 78	7½-8½	55-125	90 (MR)/55 (L)	7 (MR)/17 (L)
8-9 May 78	8½-9½	72-122	97 (MR)/72 (L)	25 (MR)/26 (L)
14-15 June 78	9½-10½	98-145	122 (MR)/98 (L)	25 (MR)/27 (L)
15-16 July 78	10½-11½	125-168	147 (MR)/125 (L)	
May$_{77}$				
1 Oct. 77	5	90-140		
5 Nov. 77	6	125-160		
14-15 Apr. 78	11½	140-160		
8-9 May 78	12	160-190		
14-15 June 78	13½	165-185		
August$_{77}$				
1 Oct. 77	2	25-85	55 (MR)	30
5 Nov 77	3	55-110	85 (M)	5
2-3 Dec. 77	4	70-118+	90 (M)	

TABLE 3.—Periods of time, sizes, and ages when spawned groups of *C. nothus* were last captured off Port Aransas and Freeport, Tex.

Spawned group and location	Period	Size (mm SL)	Age (mo)	Comments
Aug.-Sept. 76				
Port Aransas	20, 21, 28 Sept. 77	150-190	12-13	A few specimens of uncertain ID in Nov. 77 may be 14-15 mo.
Freeport	5 Nov 77	160-190	14-15	A few specimens of uncertain ID may belong to this month class.
May 76				
Port Aransas	29, 30 June 77	160-185	13	ID and sizes unclear
May 77				
Port Aransas	1 Dec. 77	115-150	7	A few specimens of uncertain ID in Mar. 78 may be 10 mo.
Freeport	14-15 June 78	165-185	13	ID and sizes unclear
Aug. 77				
Port Aransas	1 Dec. 77	75-115	4	Group not distinct after Dec. 77
Freeport	2, 3 Dec. 77	70-118	4	Group not distinct after Dec. 77
Sept 77				
Port Aransas	1 Dec. 77	40-75	3	Group not distinct after Dec. 77
Freeport	2, 3 Dec. 77	25-75	3	Group not distinct after Dec. 77
Aug.-Sept 77				
Port Aransas	8 Mar. 78	45-115	6-7	Still dominant in last collection
Freeport	15, 16 July 78	125-168	10-11	Still dominant in last collection

they approach age I. Many females were classified as early developing at 100-135 mm SL (Fig. 2). Most of the 15 fish classified as ripe or gravid were 140-170 mm SL. Age compositions and sizes at age presented later indicate that *C. nothus* mature to first spawn at 12 mo.

Silver seatrout in the northern gulf spawn from early May through late October. The collection of fish 45-55 mm SL in late June and 50-60 mm in mid-July indicates that spawning begins by early May off Port Aransas (Fig. 3). Spawning must have continued to late October, because fish 25-30 mm SL were collected from mid-August through early December. It appears that no spawning occurred from November through March or April because we captured no fish <40 mm SL after early December, and the smallest fish from February to May (Figs. 3, 4) belong to groups that were hatched before November and continued to grow through the winter.

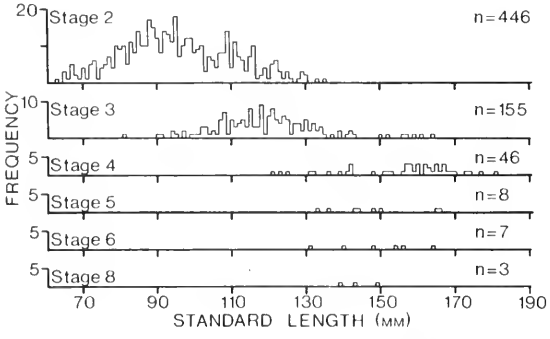

FIGURE 2.—Sizes of immature and female *C. nothus* in maturity stages two through eight. Maturity stages are 2) maturing virgin, 3) early developing, 4) late developing, 5) gravid, 6) ripe, 7) spawning/spent, and 8) resting. No stage 7 fish were caught.

Spawning occurs in two main periods each year—spring and late summer—and within each year class may produce at least three intrayear class cohorts or spawned groups, two of which may be produced in the late summer period. This is indicated by the polymodal length frequencies of fish collected off both Port Aransas (Fig. 3) and Freeport (Fig. 4), a pattern also evident in a reanalysis of Chittenden and McEachran's (1976, fig. 10) data from mid-January 1974 (Fig. 5). The polymodal frequencies do not reflect individual year classes nor do they reflect changes in size with depth. The length-frequency modes represent spawned groups that can be traced readily as follows: 1) The August$_{77}$ and September$_{77}$ groups off Freeport and Port Aransas in the period September-December 1977, 2) the August-September$_{76}$ and August-September$_{77}$ groups, which represent composites of the two individual spawned groups, in the periods February-July 1977 off Port Aransas, March 1978 off Port Aransas, and February-July 1978 off Freeport, and 3) the less distinct modes which we interpret as May$_{76}$ and May$_{77}$ groups in the periods April-June and September-December 1977 off Port Aransas and October 1977-May 1978 off Freeport. The identity of a distinct group 95-130 mm SL off Port Aransas in August 1977 is not certain. It might have hatched in spring 1977, or more probably represents survivors of the August-September$_{76}$ group. Similarly, the identity

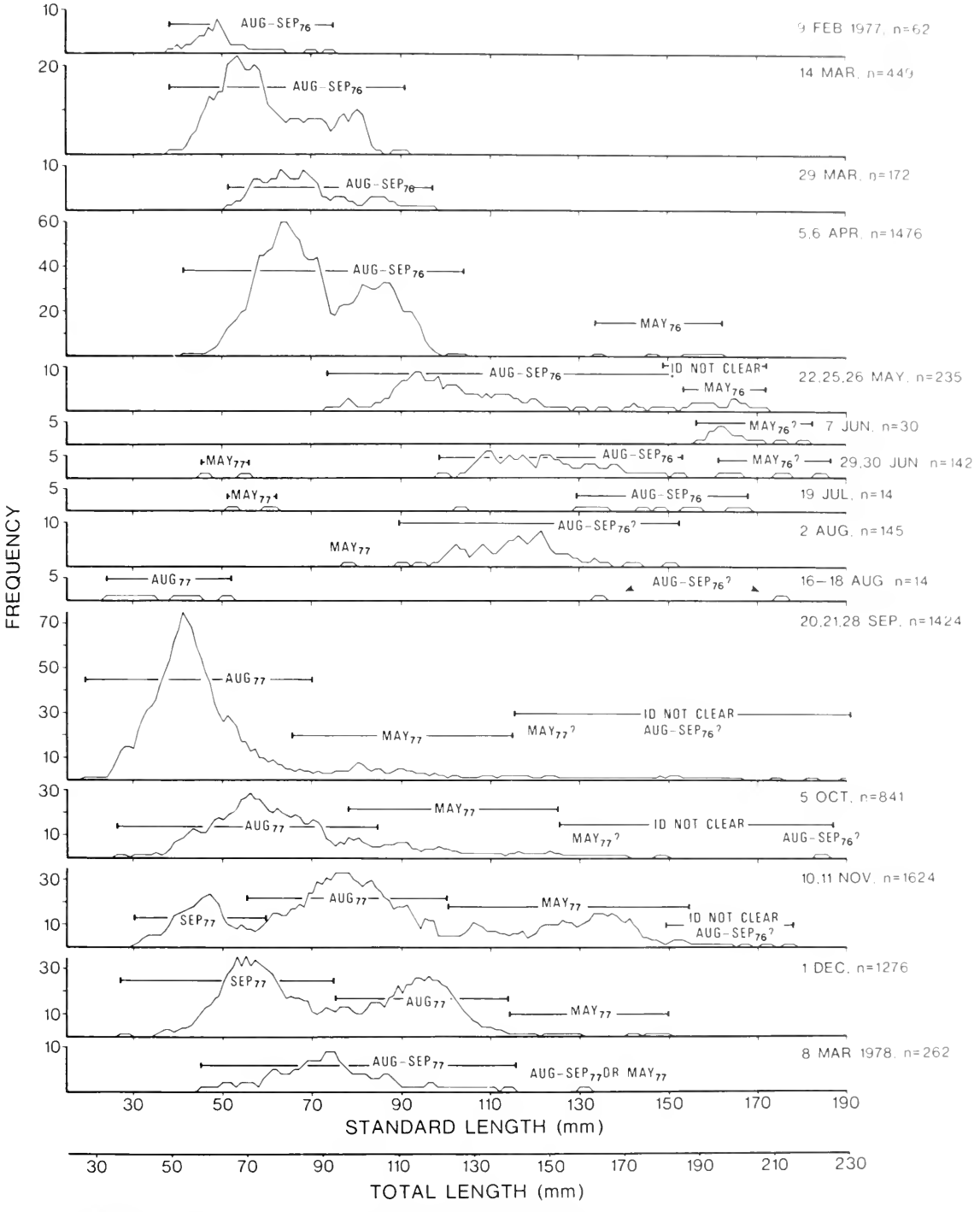

FIGURE 3.—Monthly length frequencies (moving averages of three) of *C. nothus* captured off Port Aransas. Group identity (ID) often is not clear where spawned groups meet.

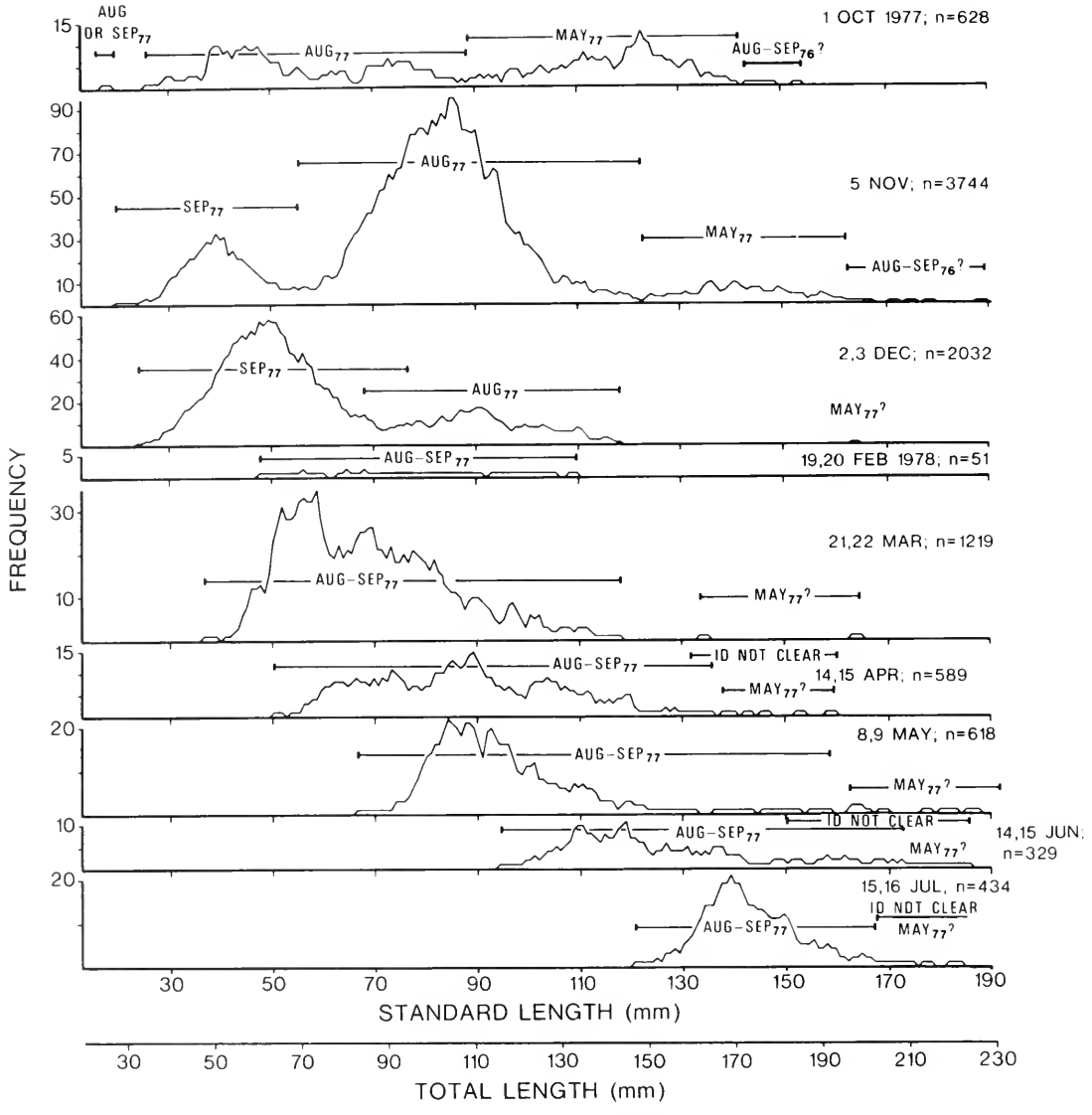

FIGURE 4.—Monthly length frequencies (moving averages of three) of *C. nothus* captured off Freeport. Group identity (ID) often is not clear where spawned groups meet.

of most large individuals off Port Aransas in fall 1977 is not certain.

Greatest or most successful spawning occurs during late summer. Many fish 25-65 mm SL were taken at 11, 12, and 29 m off Port Aransas in late September (August$_{77}$ group in Figure 3). This August-spawned group was collected at widely separated locations and formed a principal mode off Port Arnasas through early December. Fish of this size also formed a dominant mode off Freeport from October through December (August$_{77}$ group in Figure 4). Similarly, a group hatched in September formed a principal mode off Port Aransas and Freeport during November and December (September$_{77}$ group in Figures 3, 4). In contrast to these late summer groups, fish hatched in late spring did not form dominant modes.

Gonad maturity data suggest that *C. nothus* spawns from May through September in agreement with the spawning season indicated by length frequencies. Gravid or ripe females were

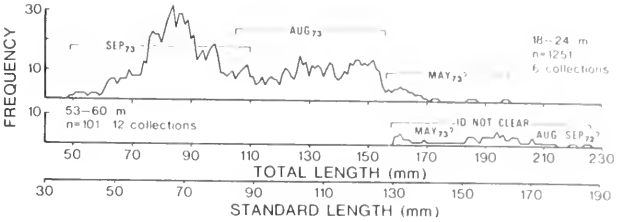

FIGURE 5.—Length frequencies (moving averages of three) of *C. nothus* captured off Freeport, Tex., 6-15 January 1974, by depth. Frequencies were reanalyzed from Chittenden and McEachran (1976, fig. 10). Group identity often is not clear where spawned groups meet.

captured during late May, June, and late September (Fig. 6), and other females 130 mm SL or larger were in the late developing stage. Some males had large gonads from May through September, and running ripe males were captured off Freeport in June and off Port Aransas in September. Females were only in the developing and resting stages in November and December, and no large females were captured from February through April.

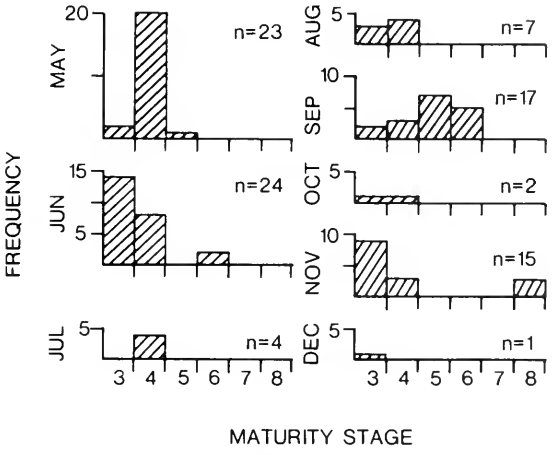

FIGURE 6.—Monthly maturity stages of female *C. nothus*. Maturity stages are 3) early developing, 4) late developing, 5) gravid, 6) ripe, 7) spawning/spent, and 8) resting.

Growth and Age Determination by Length Frequency

Only one year class of *C. nothus* occurred or dominated in any 1 mo. Fish of the 1976 and 1977 year classes occurred off Port Aransas during June, July, and August 1977 (Fig. 3). These were the only months when two year classes were clearly evident, although the comparatively few large individuals of uncertain identity in September-October 1977 probably were of a second year class. Only the 1976 and 1977 year classes occurred off Freeport from October 1977 through July 1978, but the comparatively few individuals of the 1976 year class appeared only in October and November (Fig. 4).

Cynoscion nothus reached 130-190 mm SL at age I. Fish of the dominant August and September spawned groups averaged 145-150 mm SL at 11 mo, although individuals ranged from 125 to 170 mm SL (Table 2). Similarly, the few survivors of the May groups were 130-190 mm SL at 11-14 mo. These observed sizes at age agree with the mean back-calculated length of 156 mm SL presented later.

Growth increments varied between months. The August and September spawned groups grew fastest in June and September, averaging about 25-30 mm SL/30 d (Fig. 7). Growth of recently hatched young steadily decreased from October to December and was smallest during the December-March period when increments averaged 5 mm SL/30 d. Growth increments then steadily increased to about 15-20 mm SL/30 d from March to June. The apparent pattern of greatest growth during the warm months and slowed growth during winter might be misleading. We have no growth data for the late summer period when the August-September groups

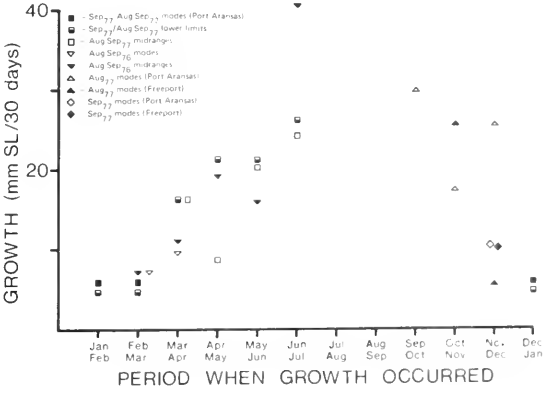

FIGURE 7.—Monthly growth increments of *C. nothus*. Unadjusted growth increments (Table 2) were adjusted to growth/30 d.

would have spawned. Growth from July through September could have been high as the apparent pattern suggests, or it might have slowed down and/or ceased as these fish matured and spawned.

Age Determination Using Scales

Silver seatrout can be aged using scales, although few fish had scales with either an annulus or false annulus. Only 38 of 1,483 fish (2.6%) had an annulus, and no fish had more than one. Only 41 fish (2.8%) had a false annulus, and they included 5 fish with an annulus. These percentages overemphasize the frequency of annuli and false annuli because the stratified sampling used to select specimens for intensive processing also selected all the large fish which would most likely show these marks.

Repeated examination suggests that age determination of *C. nothus* is consistent. We had 90% agreement in a second reading of scales from 225 fish, which included 123 fish >150 mm SL and all 38 fish first determined to have an annulus. The second reading identified an annulus in 45 specimens, including 30 of the 38 fish (79% agreement) first determined to have an annulus. The eight fish for which an annulus was not confirmed were collected in May and June about when the annulus forms; their scales had small marginal increments after an indefinite clear zone, and secondary radii and/or cutting over were not distinct. The second reading was done without knowing sizes or collection dates. This would minimize agreement between readings.

May-spawned *C. nothus* form an annulus from April (or earlier) to June when they reach 130-190 mm SL and 1 yr of age, but time of annulus formation may vary between spawned groups and is not clear for August- or September-spawned fish. Marginal increments were smallest from April to June and generally increased thereafter (Fig. 8), suggesting the first annulus forms from April (or earlier) to June. The smallest fish with an annulus was 139 mm SL and most exceeded 150 mm SL. The proportion with an annulus increased with increasing size, percentages being 16% at 150-159 mm SL ($n = 55$), 24% at 160-169 mm SL ($n = 54$), 60% at 170-179 mm SL ($n = 10$), and 100% at 180 mm SL and greater ($n = 6$). The proportion of the fish >150 mm SL with an annulus (Fig. 9) was significantly higher in May and June, when most of these large fish were May-spawned, than it was in September and November, when most were August- or September-spawned. Fish with an annulus in the period August-November all exceeded 170 mm SL and probably were survivors of the May_{76} group; those without an annulus then were 150-170 mm SL and probably August- or September-spawned.

Back-calculated lengths agree with length frequencies. Lengths at age I back-calculated using the Lee method (Lagler 1956) varied from 132 to 176 mm SL in comparison to 130-190 mm SL based on length frequencies. The mean back-calculated length was 156 mm SL with 95% confidence limits of 153-159 mm.

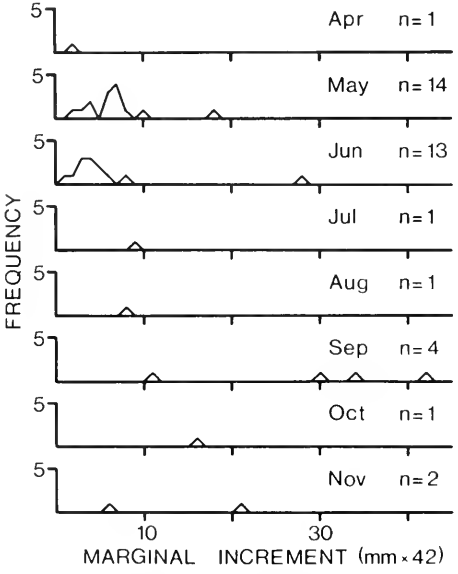

FIGURE 8.—Monthly marginal increments for *C. nothus* with one mark.

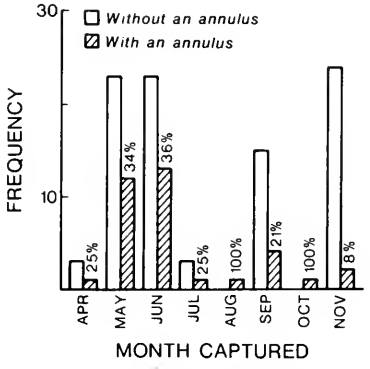

FIGURE 9.—Histogram showing by month the number and percentage of *C. nothus* >150 mm SL with and without an annulus.

Maximum Size, Life Span, and Mortality

Silver seatrout off Texas are small fish whose maximum life span (t_L) is about 1-1.5 yr. The largest of the 17,820 specimens that we captured were only 190 mm SL (230 mm TL). Almost 90% of the *C. nothus* captured off Port Aransas were <110 mm SL (Fig. 10), 99.1% were <160 mm SL, and 99.9% were <180 mm SL. Off Freeport, 85% were <110 mm SL, 99% were <160 mm SL, and 99.9% were <180 mm SL (Fig. 11). All *C. nothus* disappeared off Texas when they were slightly older than age I (Table 3).

The total annual mortality rate of *C. nothus* in the gulf off Texas approaches 100% and has a best estimate of 99.83%. Values of total annual mortality ($1 - S$) in each of the 9 mo from October 1977 through July 1978 off Freeport were 100% based on the expression $S = N_t/N_0$ where S = rate of survival and N_0 and N_t are the number of fish in consecutive year classes 0 and t. Only one year class was present off Freeport in those months so that $N_t = 0$. For the same reason, $1 - S$ was 100% off Port Aransas in each of the 4 mo from February through May 1977, during November and December 1977, and during March 1978. Mortality estimates were 98% and 99.9% for September and October off Port Aransas, assuming that fish >140 and >150 mm SL were from the older year class. For June, July, and August, $1 - S$ could not be estimated from the Port Aransas data, because the younger year class had just hatched and was incompletely recruited. However, if the predominant group in August had hatched in spring 1977, then $1 - S$ would approach 100% in that month also. Following the first procedure of Robson and Chapman (1961), we calculated an average value of $1 - S = 99.83\%$ by pooling the identifiable N_0 and N_t values for each month.

Distribution and Availability

Larger *C. nothus* seem more susceptible to trawling during the day. Few fish >100 mm SL were taken in night collections at 11, 18-24, and 29-31 m (Fig. 12), but many were taken in day collections at 7, 13-15, and 18-24 m.

Large silver seatrout almost disappeared during winter. Fish >120 mm SL from the May$_{77}$- and August-September$_{76}$ spawned groups were common during November off Port Aransas (Fig. 3) and during October and November off Freeport (Fig. 4), but very few were captured

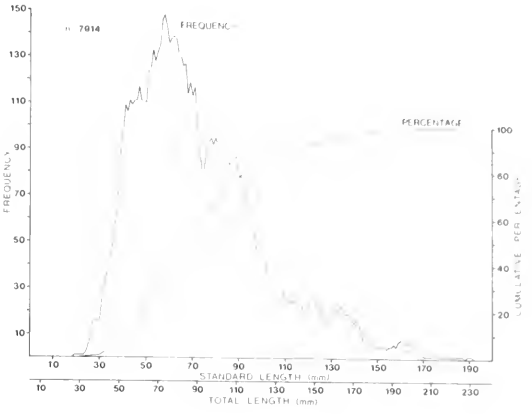

FIGURE 10.—Length frequency (moving averages of three) and cumulative percentage of all *C. nothus* collected off Port Aransas, Tex., February-December 1977.

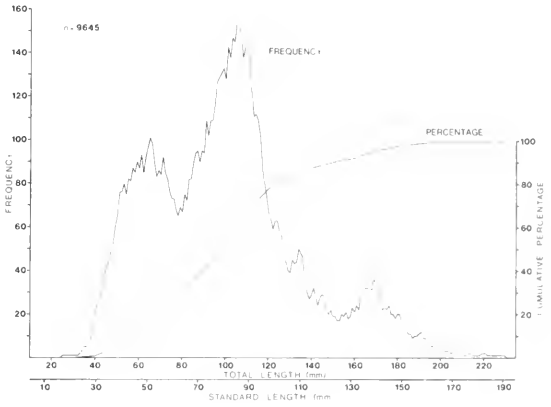

FIGURE 11.—Length frequency (moving averages of three) and cumulative percentage of all *C. nothus* collected off Freeport, Tex., October 1977-July 1978.

from December through March. The larger specimens of the August$_{77}$-spawned group also disappeared about December, which may be why the August- and September-spawned groups were not distinct thereafter. Many large fish were again taken in May or June.

Total Weight- and Girth-Standard Length and Standard Length-Total Length Relationships

Regression and related analyses for total weight-standard length, girth-standard length, and standard length-total length relationships are presented in Table 4. All regressions were

TABLE 4.—Analyses of total weight-standard length, girth-standard length, and standard length-total length relationships for *C. nothus*. Lengths and girths are in millimeters and weights are in grams.

Equation	n	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{x}$	$\bar{y}$
$\log_{10}$ TW = −4.7582 + 3.0077 $\log_{10}$ SL	2,451	0.0014	63.75	580.16	1.9056	0.9733
G = 6.64 + 0.63 SL	2,451	12.87	2,429,280	996,341	86.0	60.8
SL = −7.48 + 1.54 G	2,451	31.37	996,341	2,429,280	60.8	86.0
SL = −3.76 + 0.84 TL	303	7.48	587,667	420,074	101.5	81.8
TL = 4.98 + 1.18 SL	303	10.46	420,074	587,667	81.8	101.5

significant at $\alpha = 0.01$. Coefficients of determination (100 r^2) were 97% for girth-standard length relationships but 99% for total weight-standard length and standard length-total length relationships. All relationships were based on fish whose standard length range was 26-188 mm.

DISCUSSION

Spawning

Our findings on *C. nothus* reproduction agree with the limited literature. The finding of spawning from May to late October is consistent with reports of 1) fish about 35-40 mm TL (26-30 mm SL) or smaller from June to December (Hildebrand and Cable 1934; Hoese 1965; Christmas and Waller 1973; Mahood 1974), 2) ripe individuals in mid-May (Miller 1965) and throughout August (Gunter 1945; Hildebrand 1954), and 3) late-developing specimens in August and September (Mahood 1974). Our finding of peak spawning in late summer agrees with Gunter (1945) and Chittenden and McEachran (1976), and with the dominance of a late summer-spawned group in Mahood (1974, fig. 13). The small size at maturity is consistent with Miller's (1965) report of running ripe females only 135-140 mm TL (110-114 mm SL), although the smallest fish that Mahood (1974) collected in late-developing or spent condition was 205 mm TL (168 mm SL). Our finding of May-, August-, and September-spawned groups is similar to the spring peak and late summer or fall peak of reproduction reported for *C. nothus* (Mahood 1974) and for *C. arenarius* (Shlossman and Chittenden 1981). The latter workers suggested that the spawning periodicity of *C. arenarius* was timed to coincide with the two major periods of rising sea level in the northern Gulf of Mexico each year when surface currents could transport eggs and/or larvae to inshore or estuarine nurseries. Spawning of *C. nothus* in the Gulf of Mexico probably is timed also to take advantage of such current transport. We have observed that *C. nothus* exhibits two distinct peaks of spawning within the August-September major spawning period. It is not yet clear 1) whether multiple-spawned group production consistently occurs within the late summer reproduction period, which would imply spawning keyed to regular intraperiod cues, or 2) whether multiple-spawned group production in the late summer period reflects irregular happenstances such as the increased survival and recruitment that could occur if reproduction at times coincided with unusually favorable current transport (Hjort 1914, 1926; Nelson et al. 1977), or if a critical larval period (Marr 1956; May 1974) irregularly coincided with an unusually great food supply.

Growth and Age Determination

Our estimates that *C. nothus* in the northern Gulf of Mexico reach 130-190 mm SL and average 150 mm or more when they disappear at age I agree with Chittenden and McEachran (1976) and Chittenden (1977) that *C. nothus* reaches 120-150 mm SL (150-185 mm TL) at age I. Gunter's (1945) estimate that fish 75-110 mm SL (93-138 mm TL) taken in May were about 1 yr old is low and may have been based on fish that actually would not have reached age I until the major spawning period of August-September. None of these cited workers, though, recognized the multiple-spawned group composition of this species and their estimates of age could be in error. Our estimates for *C. nothus* agree with estimates for *C. nebulosus* of 157-165 mm SL at age I (Pearson 1929; Moody 1950; Tabb 1961), although lower estimates of 116 and 130 mm SL have been reported (Klima and Tabb 1959; Moffett 1961). The growth of *C. nothus* also agrees with estimates for *C. regalis* of 143-180 mm SL at age I (Merriner 1973). Seasonal growth of August-September spawned *C. nothus* appears comparable to that of *C. nebulosus* and *C. regalis*. Pearson (1929) found

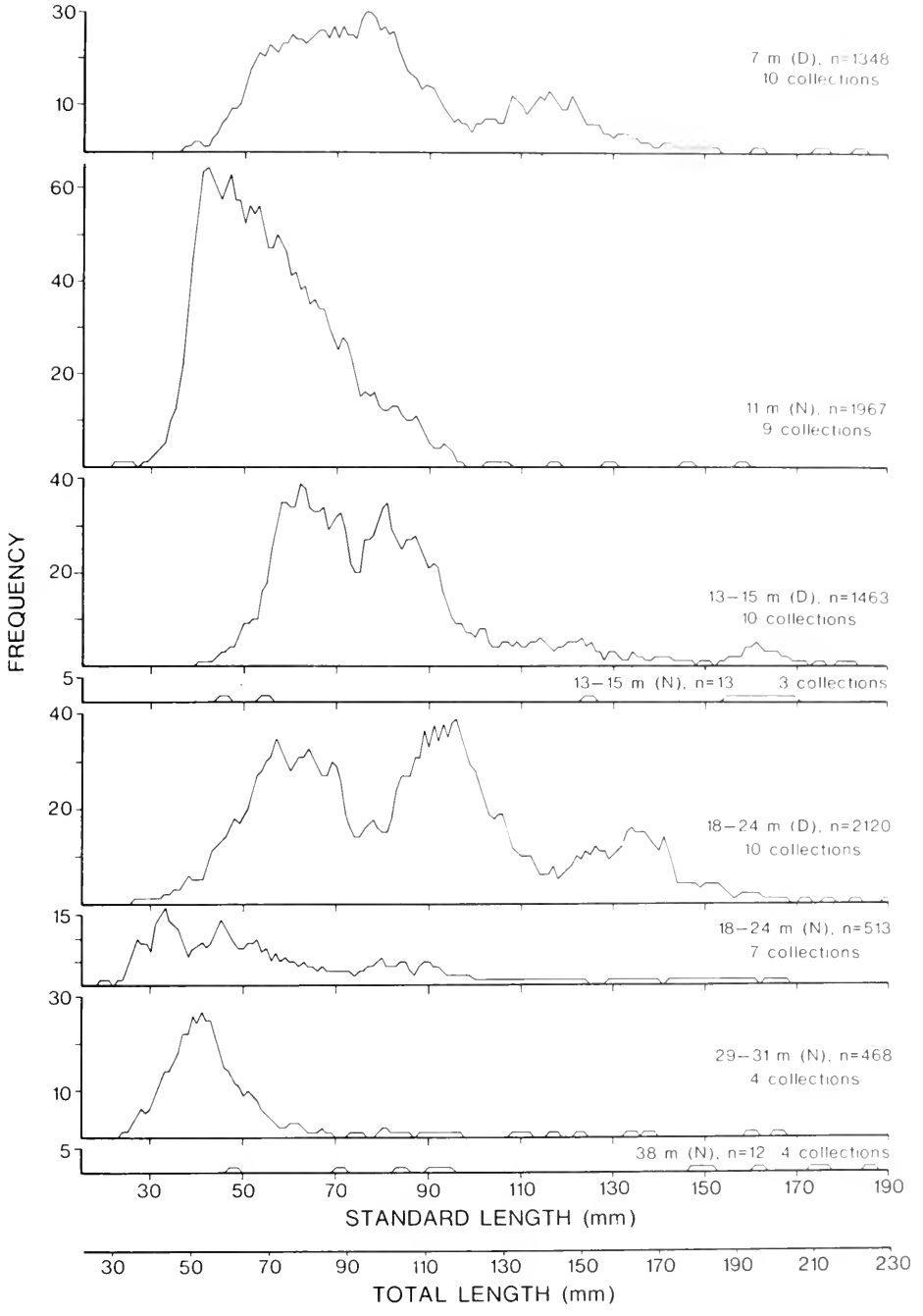

FIGURE 12.—Pooled length frequencies (moving averages of three) of *C. nothus* collected by day (D) and night (N) off Port Aransas, Tex., at each depth.

a similar seasonal growth pattern for *C. nebulosus* from Texas, but he did not calculate monthly increments. Estimates of monthly growth for *C. regalis* at age 0 are about 30-55 mm TL during the summer (24-45 mm SL) and about 10 mm TL in October (Welsh and Breder 1923; Hildebrand and Cable 1934; Pearson 1941).

Scales can be used to age *C. nothus*, but age de-

termination would probably be as accurate from intensive length frequencies alone. The long spawning season and multiple-spawned group compositions complicate age determination. Exact age determination may be difficult for the few fish age II or older. The few fish of these ages might not be distinct in length frequencies and a spawned group probably could not be assigned. Growth and mortality estimates for *C. nothus* should be based upon individual spawned groups to avoid misinterpretation.

Maximum Size, Life Span, and Mortality

The largest specimen of *C. nothus* that we captured (190 mm SL = 230 mm TL) is similar to the maximum sizes typically reported (Hildebrand and Cable 1934; Gunter 1945; Hildebrand 1954; Christmas and Waller 1973; Chittenden and McEachran 1976). The only published records of fish much >190 mm SL include a specimen 315 mm SL (380 mm TL) from the Gulf of Mexico off Mississippi (Franks et al. 1972), a few specimens to 259 mm SL (312 mm TL) from industrial fish catches in the gulf (Thompson 1966), and Mahood's (1974) report of two fish 255 mm SL (308 mm TL) from the Atlantic Ocean off Georgia. Net avoidance and/or behavioral change to a midwater life-style probably does not explain the absence of *C. nothus* >190 mm SL off Texas, because we collected many *C. arenarius* to 283 mm SL. Large *C. nothus* apparently do not occupy water deeper than 46 m off Texas, because twice monthly day and night collections at 55-100 m in the period June 1979-August 1980 have not captured larger fish (Chittenden, unpubl. data). The absence of large *C. nothus* off Texas might indicate movement to rough, normally untrawled substrate or possibly a spawning or postspawning movement to the northcentral gulf. Large *C. nothus* to 225-250 mm SL occur in deep water in the northcentral gulf (E. Gutherz and B. Rohr[6]), but the comparative percentage of these large fish needs further study. Based on our data and the published literature, however, it appears that *C. nothus* does not exist in significant numbers at sizes >190 mm SL. Even Mahood's (1974) data indicate that only 4% of his specimens were >188 mm SL.

[6]E. Gutherz and B. Rohr, Fishery Biologists, Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service, NOAA, Pascagoula, MI 39567, pers. commun. January 1981.

The maximum life span of *C. nothus* is only 1-1.5 yr off Texas, although it might be as long as 2 yr in the northcentral gulf or off the southeast United States. A value of t_L = 1-1.5 yr seems reasonable for Texas waters because fish >160-180 mm SL (the average size at age I) made up <1-0.5% of our catch. Our estimate is supported by the absence of fish with more than one annulus and by the complete disappearance of fish after age I. This agrees with Chittenden and McEachran's (1976) estimate that the life span is little more than 1 yr. A t_L value as large as 2.0 yr seems tenable only for Mahood's (1974) data and, possibly, for the northcentral gulf where some fish reach larger sizes than we observed.

Our observed mortality estimates agree with theory (White and Chittenden 1977; Royce 1972: 238) that the total annual mortality rate is 90-100% if the life span is only about 1-2 yr. Our best estimate that $1 - S$ is 99% may be a slight overestimate, particularly if large fish exhibit significant spawning or postspawning migration to the northcentral gulf. However, it seems unlikely that many fish survive beyond 2 yr and that $1 - S$ is <90%. This is supported by Mahood's (1974) data which suggest a 96% mortality rate for *C. nothus* off the southeast coast of the United States, assuming that all his specimens >188 mm SL were age II fish. The high mortality rate that we have found explains why few *C. nothus* had an annulus. Most fish probably die before or while a mark forms on the scales.

Distribution and Availability

The disappearance of large *C. nothus* that we found during winter agrees with Mahood (1974, table 8), who reported only six specimens (of 947 fish) >130 mm SL (160 mm TL) from October through April, and with Hildebrand and Cable (1934), who reported no *C. nothus* captured off Beaufort Inlet, N.C., during winter although they were rather common in summer. The disappearance of large *C. nothus* during the colder months and their subsequent reappearance in spring probably reflects an offshore overwintering movement of large fish. This interpretation is supported by 1) reanalysis of Chittenden and McEachran's (1976, fig. 10) data on distribution of *C. nothus* in mid-January (Fig. 5) which indicates that fish >140 mm SL were most abundant in deep water, and 2) Miller's (1965) report that large *C. nothus* occurred in deep water from February through April.

General

The production of several spawned groups over a broad time period in each annual spawning season is extremely important to the population dynamics of *C. nothus*. This species is short-lived and appears little more than an annual crop whose abundance could fluctuate greatly from year to year. However, the multiple-spawned group structure would buffer against population instability just as a multiple year class structure buffers population size in longer lived species. The multiple-spawned group feature may average over a longer period each year the effects of environmental variation on spawning success, may dampen fluctuations in annual spawning success associated with environmental extremes, and may stabilize population sizes. Similarly, the effects of fishing would be averaged over a greater number of spawned groups in 1 yr, so that the multiple-spawned group structure might minimize the possibility of recruitment overfishing. In that event, stock assessments based on dynamic pool models and growth overfishing would be more valid.

Many features of the population dynamics of *C. nothus*—short life span, high mortality rate, and rapid turnover of biomass—are similar to those in the Atlantic croaker, *Micropogonias undulatus*, of the Carolinean Province (White and Chittenden 1977; Chittenden 1977). This supports the suggestion (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the gulf have evolved towards a common pattern of population dynamics. Because of their similar population dynamics, the implications of Chittenden's (1977) simulations on croaker could serve as a first approximation of the effects of harvesting *C. nothus*, so that this species also should have a great biological capacity to resist growth overfishing.

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CYCLOGRAPSUS INTEGER H. MILNE EDWARDS, 1837 (BRACHYURA, GRAPSIDAE): THE COMPLETE LARVAL DEVELOPMENT IN THE LABORATORY, WITH NOTES ON LARVAE OF THE GENUS *CYCLOGRAPSUS*

ROBERT H. GORE AND LIBERTA E. SCOTTO[1]

ABSTRACT

The complete larval development of *Cyelograpsus integer*, a small sesarmine grapsid crab, is described and illustrated from larvae reared in the laboratory. *Cyelograpsus integer* attains five, and often six, zoeal stages plus one megalopal stage. Temperature affects both duration of larval development and number of larval stages. At 25°C, the megalopal stage was attained in 26-27 days from fifth stage zoeae and 31-32 days from sixth stage zoeae, while metamorphosis at 20°C occurred in 53-55 days from sixth stage zoeae. The zoeal and megalopal stages of *C. integer* are compared to all known cultured species of the genus and morphological differences are noted. *Cyelograpsus integer* zoeae may be distinguished from both other species in the genus and other species in the family by its antennal morphology, being the only species with the type A antenna (i.e., the exopodite about equal in length to the protopodite). Megalopae of this species may be distinguished from other species in the genus by the formation of the frontal region and the terminal setation of the telson. Other potentially useful zoeal morphological characters are discussed regarding both the taxonomic and phylogenetic position of *C. integer*.

The sesarmine genus *Cyclograpsus* is cosmopolitan, containing at least 16 species, 13 of which occur in the Indo-West Pacific region (Griffin 1968). *Cyclograpsus integer*, one of four species in the genus occurring in the New World and the only one known from the western Atlantic, is quite widespread with records from western and eastern Africa, and localities in the Indo-West, eastern central, and northern west Pacific Ocean (Monod 1956; Griffin 1968; Manning and Holthuis 1981). Although Rathbun (1918) listed the Peruvian and South American species *Cyclograpsus cinereus* Dana, 1851 as being the eastern Pacific analog to *C. integer*, Griffin (1968) noted that *Cyclograpsus escondidensis* Rathbun, 1933, an eastern Pacific species known only from Central America, was closer to *C. integer* than to any other member of the genus. In the same study, Griffin described *Cyclograpsus sanctaecrucis*, a new species from Santa Cruz Island in the southwestern Pacific Ocean, stating that "Except in the presence of a lateral notch on the carapace, [this] species most closely resembles *C. integer*." Thus, *Cyclograpsus integer* appears similar to at least two other species in the genus from the Pacific Ocean.

The larvae of members of the genus are not well known, and the complete larval development has been determined for only two New World species at present. Costlow and Fagetti (1967) described and illustrated the complete development of *C. cinereus* from Chile, and in a subsequent paper Fagetti and Campodonico (1971) recorded the development of a species from Juan Fernandez Islands which they identified as *Cyclograpsus punctatus* H. Milne Edwards, 1837. Griffin, however (1968), suggested that specimens of *Cyclograpsus* from those islands are actually referable to *Cyclograpsus lavauxi* H. Milne Edwards, 1837, stating that *C. punctatus* is restricted to South Africa. To add to this confusion, Wear (1970) described and illustrated the first zoeal stages of two New Zealand species, *Cyclograpsus insularum* Campbell and Griffin, 1966, and *C. lavauxi*. But a comparison of his illustrations of the latter species with the first zoeal stage figured by Fagetti and Campodonico shows substantial differences in the number and position of chromatophores, appendage processes, and segmentation of the maxillule, suggesting that notable variation occurs between eastern and western Pacific populations of *C.*

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lavauxi, if Fagetti and Campodonico's species was misidentified. These differences raise the possibility that the New Zealand (Wear 1970) and Chilean (Fagetti and Campodonico 1971) forms of *C. lavauxi* are subspecies, assuming that Griffin is correct in restricting *C. punctatus* to South Africa. On the other hand, the Chilean specimens may indeed have been correctly identified as *C. punctatus*, thus accounting for the observed differences in the larvae, as well as reinstating the Juan Fernandez Islands as the westernmost zoogeographical boundary for the species. Until further data are available, we will consider Fagetti and Campodonico's species to be correctly identified as *C. punctatus*, so that we may compare the morphological features of this species with others in the genus.

The aforementioned confusion, and the widespread occurrence of *C. integer*, as well as its close morphological relationship to *C. escondidensis*, its Central American analog, all illustrate the importance of determining the larval development of these species. Accomplishing this would facilitate identification of their respective larvae in the plankton and also allow comparisons of morphological features in zoeal and megalopal stages. The latter stages provide a means of elucidating phylogenetic relationships both intra- and intergenerically among the Grapsidae. Accordingly, in this paper we describe and illustrate the complete larval development of *Cyclograpsus integer* and compare salient characters shared by the zoeae and megalopae in *C. punctatus*, *C. cinereus* from the New World, and *C. lavauxi* and *C. insularum* first zoeae from the Indo-West Pacific.

MATERIALS AND METHODS

Three ovigerous females (carapace width 7.0, 9.3, 10.4 mm) were collected among medium-sized cobbles in the high intertidal zone at Bodden Town, Grand Cayman Island, on 15 July 1980. Following previous methodology (Gore 1968), the crabs were maintained in 19 cm diameter glass bowls filled with seawater (34‰) and fed *Artemia* spp. nauplii daily until hatching occurred on 25, 28, and 29 July 1980 (largest to smallest female, respectively). A total of 192 larvae were cultured in eight 24-compartmented polystyrene trays, one larva per compartment. The eight trays were maintained in controlled temperature units in a diel fluorescent light cycle of 12 h light, 12 h dark. A total of 144 larvae (72 at each temperature) were cultured at 20° and 25°C (±0.5°C). Another 48 larvae were maintained at 15°C (±0.5°C). Seawater (34-36‰) was changed and the larvae were fed *Artemia* nauplii daily. All dead larvae, molts, and representative live specimens were preserved in 70% ethanol. Descriptions and illustrations were made with the aid of dissecting stereomicroscope and compound microscope with camera lucida attachments, using specimens from all three hatches. Measurements are the arithmetic mean of all specimens examined in a given stage. Carapace length was measured from the base of the rostrum to the posterior margin of the carapace, lateral view in zoeae and dorsal view in megalopae. Carapace width in the latter was measured dorsally across the widest part of the carapace. In all descriptions, setal formulae progress distally.

The first 4 zoeal stages are denoted as ZI to ZIV. One series of fifth zoeal stages (ZVu; ultimate) molted directly to megalopa stage; another (ZVp; penultimate) molted to a sixth (ZVI) stage. The morphological differences in these two forms are noted in the text.

A complete larval series and/or their molts is deposited in the National Museum of Natural History, Washington, D.C. (USNM 184669); the Allan Hancock Foundation, University of Southern California, Los Angeles (AHF 2328-1); the British Museum (Natural History), London (1981-447); the Rijksmuseum van Natuurlijke Historie, Leiden (D-34220); the Museum National d'Histoire Naturelle, Paris (M.N.H.N.-B7294, 7295); and the Indian River Coastal Zone Museum, Fort Pierce, Fla. (IRCZM 89:5096). The adult females are divided among the National Museum of Natural History, the Indian River Coastal Zone Museum, and the Paris Museum.

RESULTS OF THE REARING EXPERIMENT

Temperature not only influences the duration of larval development within stages, but also affects the number of zoeal stages attained (Table 1, Fig. 1). At the warmer temperature (25°C) either 5, or occasionally 6, zoeal stages occurred. However, the single first crab stage was reached after 37 d in the laboratory by a megalopa which molted from a stage V zoea. Of 3 other stage V zoeae that molted to stage VI, only 2 eventually reached megalopa and none sur-

TABLE 1.—Duration in days of larval and postlarval stages in *Cyclograpsus integer* at two laboratory-culture temperatures. (Mean based only on larvae attaining next stage.)

Temperature (°C)	Stage	Minimum	Mean	Mode	Maximum	Number molting to next stage (or dying in molt)
25	Zoea I	5	6 6	6	11	44
	II	4	4 3	4	6	22 (+2)
	III	4	4 2	4	6	18
	IV	4	4 2	4	5	14
	Zoea V-Megalopa	4	5.2	6	6	5 (+2)
	Zoea V-VI	4	4 0	4	4	3
	Zoea VI-Megalopa	6	6.0	6	6	2
	Megalopa (V)	11	—	—	—	1
	Megalopa (VI)	All died in stage after 1 day				0
20	Zoea I	9	10.9	10 (13)[1]	14 (21)[1]	21 (+1)
	II	7	9.2	8	17	14
	III	6	7.3	8	9	13
	IV	7	7.9	8	9	10
	Zoea V-Megalopa	No fifth stage zoeae molted to megalopa				
	Zoea V-VI	6	7.7	7-8	12	9
	Zoea VI-Megalopa	11	11 7	12	12	6 (+1)
	Megalopa	18	21 7	—	25	3

[1]Died in stage.

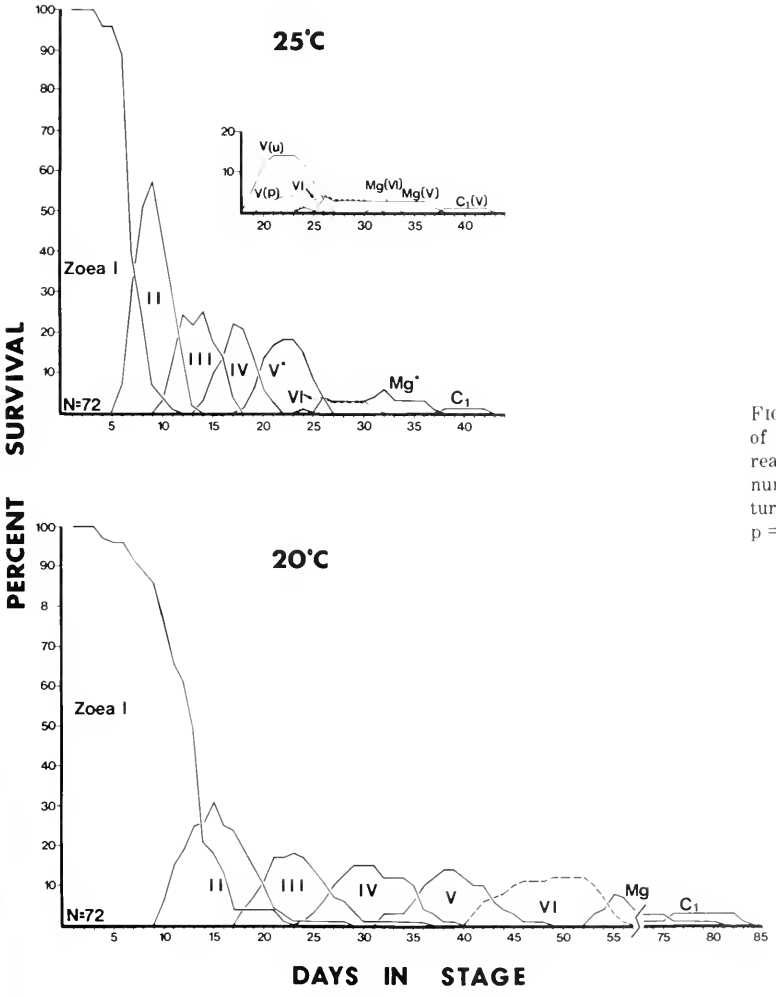

FIGURE 1.—Percent survival and duration of larval stages in *Cyclograpsus integer* reared under laboratory conditions. N = number of larvae cultured at each temperature; * = combined stages; u = ultimate stage; p = penultimate stage. [See text.]

vived to first crab stage. The time period of 37 d may well be a reasonable reflection of what takes place in the plankton, because at 25°C in the laboratory a hypothetical zoea passing through the minimum duration for each stage could conceivably attain first crab stage in as few as 32 d (5 stages) or 38 d (6 stages) after hatching.

The variation in duration of each zoeal stage at 25°C (except for the first zoea) was rather low, comprising no more than 2 d. Stage I, however, could last from 5 to 11 d, although most individuals molted to stage II between 6 and 7 d after hatching. A single zoea that remained in stage I for 11 d also molted to stage II, but died the following day. A comparison of the values in Table 1 with the survival graph (Fig. 1) shows that mortality was quite high on the days just prior to, and during, the ecdysial period in stage I, but as development progressed the mortality subsequently fell. These results are similar to others obtained in our laboratory with brachyuran and anomuran larvae, and indicate that the more mature zoeal stages have a greater survival potential. This might be a result of one or a combination of factors, including the type, quality, and amount of food consumed, the genetic makeup of the parents, or a response by the larvae to unfavorable physical conditions in the laboratory (see Bookhout and Costlow 1970; Knowlton 1974; Gore et al. 1981, for summaries of the various hypotheses).

At 20°C, both within-stage and overall developmental duration were more variable. Extended zoeal durations and the production of a sixth zoeal stage were both noted at the cooler temperature. Larvae remained in stage I 9-14 d before proceeding with further development. Most larvae molting to stage II did so 10 d after hatching. However, a larger component of zoeae died than survived during this ecdysis, most dying at day 14, with 3 zoeae lasting until day 21. It would seem that whatever general effect the lower temperature has on zoeal stages cannot be overridden after about 12-13 d in the first stage, so that the larvae eventually die if they have not molted by this time. Once stage II was reached, most zoeae were capable of continuing their development with relatively little mortality compared to that seen in stage I (Fig. 1). Modal values of within-stage developmental time were generally twice that seen at 25°C. The rearing data also show that the megalopal stage was attained following 6, rather than 5, zoeal stages, approximately 53-55 d after eclosion. Another 18-25 d were required before the first crab stage was reached. Thus, a minimum of 73 d was required after hatching to complete development, even though an extrapolation from the minima in Table 1 suggests that a hypothetical zoea might possibly reach first crab stage in as few as 64 d after hatching at 20°C. Extended developmental times such as these are not necessarily detrimental if the larvae can avoid predation and find sufficient and suitable food. Such longer periods of development could aid in the dispersal of the larvae, thereby accounting, at least in part, for the wide distribution of the adults of this species. However, at the lower temperature of 15°C, all of the 48 larvae remained in stage I up to 12 d before dying. This high mortality suggests very unfavorable conditions for the survival of this species.

Cyclograpsus integer, along with some species of *Sesarma*, is among the few Sesarminae, and among still fewer Varuninae and Plagusiinae (Wilson 1980; Wilson and Gore 1980) known to have extra larval stages. The species presently stands alone in the genus in having this feature, but joins an increasingly large group of brachyuran (and anomuran) crustaceans in which an additional larval stage occurs either at lower, or perhaps suboptimum, temperatures (Sandifer 1973; Knowlton 1974; Scotto 1979; Gore et al. 1981). The studies just cited follow classic investigations by Costlow et al. (1960), Bookhout (1972), and Bookhout and Costlow (1974) in which temperature and salinity were manipulated and the effects on survival, duration, and number of larval stages were observed. The data in all these studies add to a large body of circumstantial evidence from the plankton (e.g., alleged substages, morphological variants, oversized larvae, etc.) which suggests that additional larval stages may be an integral part of a decapod crustacean's larval potentiality in nature, and not just an artifact observed during laboratory culture of the species. Whether extra stages occur commonly, or only rarely, they are still classifiable as a response to change in conditions, and as such constitute an evolutionary adaptation toward survival.

Description of the Larvae

First Zoea

Carapace length: 0.38 mm; 5 specimens examined.

Carapace (Fig. 2A, a).—Smooth, globose, dorsal spine short, slightly curving posteriorly, rostral spine stout, bluntly rounded, ventrally directed; no lateral spines present in this stage. A mediodorsal knob (Fig. 2a) midway between bases of dorsal and rostral spines with 5 integumental sensilla arranged as illustrated, these present in all stages. Posterolateral margin of carapace indistinctly and irregularly dentate; ventrolateral margin produced into a blunt V-shaped process. Paired setae posterolaterally to base of dorsal spine in all stages. Eyes unstalked.

Abdomen and Telson (Fig. 2B).—Five somites; first naked, second, third, and fourth with paired lateral knobs (fourth smallest) directed anteriorly, ventrally, and laterally respectively, these also with bluntly rounded posterolateral process; fifth somite with bluntly rounded posterolateral process. Pair of posterodorsal setae on somites 2-5 in all stages. Telson rectangular with pair of short, minutely hairy, furcae, 6 spines in between, each armed with rows of spinules. Shallow median notch present.

Antennule (Fig. 2C).—Conical rod directed anteriorly, flanking rostral spine, with 4 aesthetascs of varying size.

Antenna (Fig. 2D).—Biramous; protopodite and exopodite spinelike processes approximately equal in length, both armed with 2 rows of spinules; exopodite with a simple seta one-third distance from base.

Mandibles (Fig. 2E).—Asymmetrically scoop-shaped process; incisor process with 1 large tooth anteriorly as well as posteriorly, 3 bluntly rounded denticles in between, plus 3 similarly on posterior edge of right mandible, 2 on left; molar process irregularly dentate, a large rounded tooth on the posterior angle.

Maxillule (Fig. 2F).—Endopodite 2-segmented, setal formula progressing distally 1,5 (4 terminal plus 1 subterminal); basal endite with 5 stout setae, coxal endite with 4 stout, 1 thinner seta. Additional pubescence as illustrated.

Maxilla (Fig. 2G).—Endopodite irregularly bilobed, each with 2 setae; basal and coxal endite bilobed, setal formula proximally to distally 5,4 and 4,3, respectively. Scaphognathite with 4 plumose setae on outer margin, distal portion tapering to setose apical process. Other pubescence as illustrated.

Maxilliped 1 (Fig. 2H).—Coxopodite naked; basipodite with 9 ventral setae, progressing distally 2,2,3,2; endopodite 5-segmented, setal formula 2,2,1,2,4+I (Roman numeral = dorsal setae), third segment with several minute hairs on dorsal surface; exopodite indistinctly 2-segmented, 4 terminal natatory setae.

Maxilliped 2 (Fig. 2I).—Coxopodite naked; basipodite with 4 ventral setae, progressing distally 1,1,1,1; endopodite 3-segmented, setal formula 0,1,5+I; exopodite indistinctly 2-segmented, 4 natatory setae.

Color.—Overall golden-brown under refracted light, abdomen colored more intensely than cephalothorax. Cornea black under refracted, iridescent blue under reflected light. Grouped brown and orange chromatophores appear as follows: carapace, 4 interocular, 1 at base of dorsal spine, 1 at position of posterodorsal knob, 2 at future position of lateral spines, 4 along posterior margin, 3 at posteroventral angle; appendages, 1 on mandibles, 1 each on antennular and antennal protopodites, 2 on each maxillipedal basipodite; abdomen, 1 pair ventromedially on first somite, second through fifth somites with 1 pair anteroventrally and 1 pair posteroventrally; telson with 1 pair anteriorly and 1 pair posteriorly at base of each set of 3 spines.

Second Zoea

Carapace length: 0.50 mm; 5 specimens examined.

Carapace (Fig. 3A).—Enlarged, pair of ventrally curved lateral spines now present. Dorsal and rostral spines both elongated, thinner, ends more tapered than first stage. Pair of interocular and 1 posterolateral seta now present. Posterodorsal knob midway between base of dorsal spine and posterior edge of carapace more prominent. Eyes stalked.

Abdomen and Telson (Fig. 3B).—Similar in shape and armature to first stage with addition of single long dorsal seta on posteromedial edge of first somite.

Antennule (Fig. 3C).—As in first stage but with 6 unequal aesthetascs.

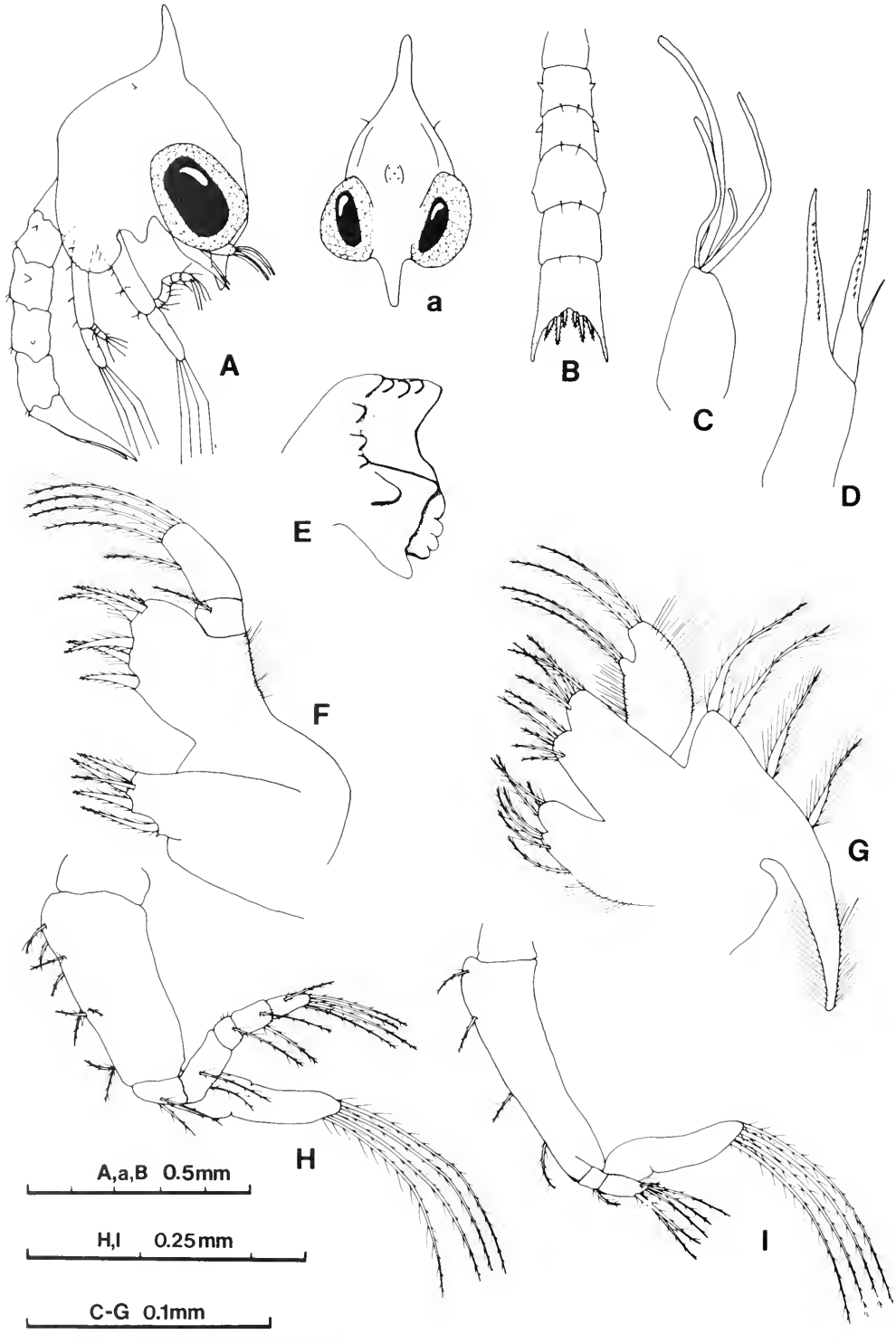

FIGURE 2.—First zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (a) anterodorsal view; (B) abdomen and telson (in dorsal view as illustrated here and throughout all stages); (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

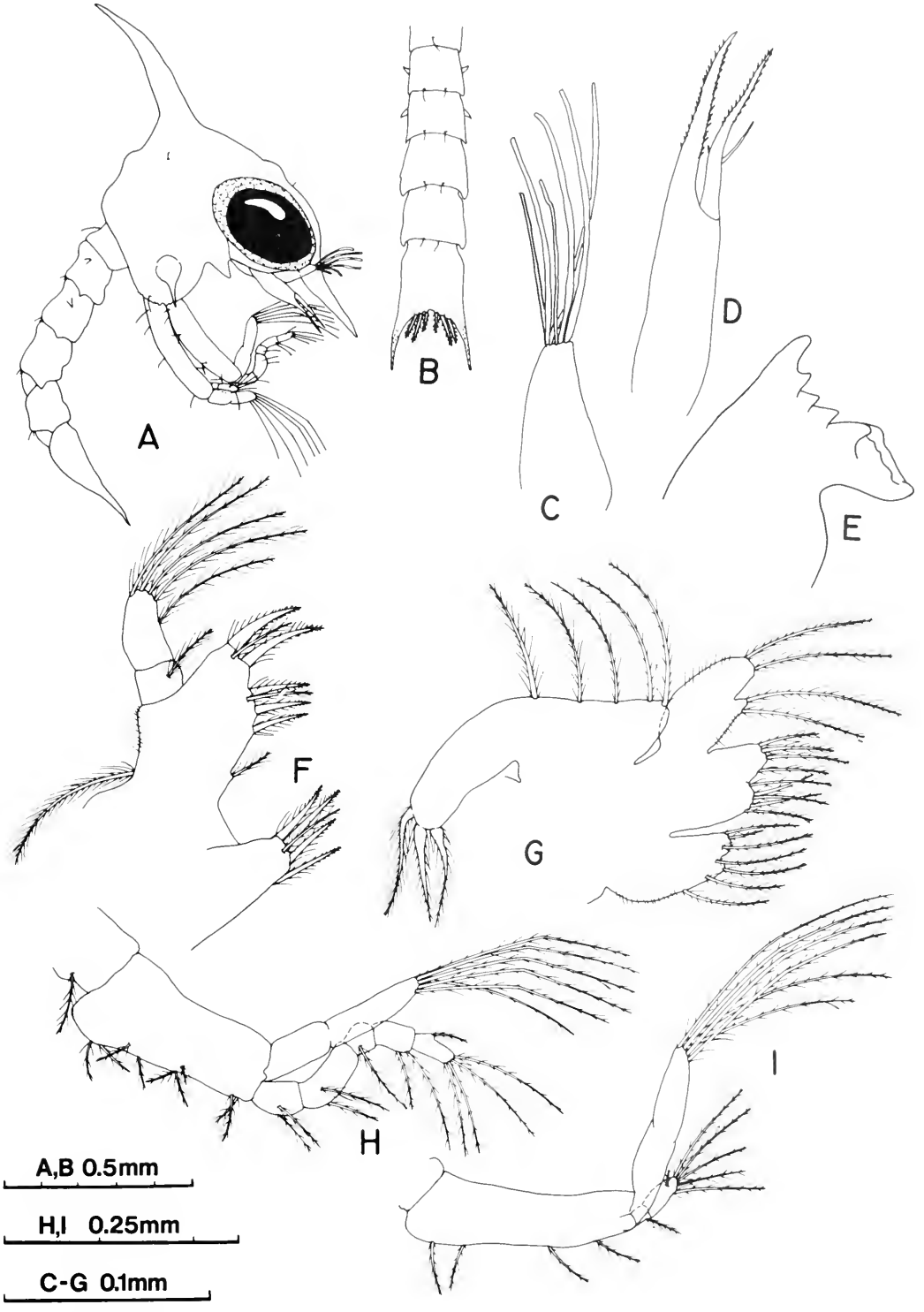

FIGURE 3.—Second zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

Antenna (Fig. 3D).—Similar in form and armature to first stage, with addition of minute hair on exopodite opposite of simple seta one-third from base.

Mandible (Fig. 3E).—Increased in size, shape and armature similar to first stage.

Maxillule (Fig. 3F).—Endopodite and coxal endite setation unchanged. Basal endite now with 5 stout, 3 thinner setae plus 1 long plumose seta on basal margin.

Maxilla (Fig. 3G).—Endopodite, basal, and coxal endite setation unchanged. Scaphognathite with 5 long, thin, plumose setae proximally, 3 stout plumose setae on distal margin.

Maxilliped 1 (Fig. 3H).—Coxopodite with 1 ventral seta. Basi- and endopodite setation unchanged. Exopodite with 6 natatory setae.

Maxilliped 2 (Fig. 3I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite now with 6 natatory setae.

Color.—Overall darker golden brown than first stage. Color much more intense at dorsal spine, fifth somite, and telson. Lateral spines, rostrum, maxillipedal endo- and exopodites transparent. Deep golden hue around base of dorsal spine. Other chromatophore color and position as in first stage.

Third Zoea

Carapace length: 0.70 mm; 5 specimens examined.

Carapace (Fig. 4A).—Zoea much enlarged, dorsal, rostral, and lateral spines elongate, 2 pair of interocular setae, posterodorsal knob more prominent, posterolateral margin now with 4 or 5 setae placed as illustrated, irregular denticulation ventral to setae present here and in all stages. Posterodorsal margin of carapace with 3 setae.

Abdomen and Telson (Fig. 4B).—Sixth abdominal somite now present, with small bluntly rounded posterolateral process. First somite with 3 dorsomedial setae, middle the longest. Paired lateral knobs on second and third somites enlarged, posterolateral processes on somites 2-5. Telson with interfurcal setal formula now 4+4, innermost pair the shortest.

Antennule (Fig. 4C).—Unchanged in form from second stage, with 4 unequal aesthetascs.

Antenna (Fig. 4D).—Similar to second stage, exopodite now slightly shorter than protopodite.

Mandible (Fig. 4E).—Similar in form and armature to second stage.

Maxillule (Fig. 4F).—Endopodite and basal endite armature unchanged, 1,5 and 8+1 processes basally, respectively. Coxal endite with 5 setae plus 1 long plumose seta on basal margin.

Maxilla (Fig. 4G).—Endopodite 2,2, as before, basal endites 5,4, coxal endites now 5,3. Scaphognathite setae increased to 10 thinner plus 6 stout distal setae, separated by sparse hairs as illustrated.

Maxilliped 1 (Fig. 4H).—Coxo- and basipodite setation unchanged. Endopodite setal formula now 2,2,1 plus spine replacing dorsal setae, 2, 4+I. Exopodal natatory setae 8.

Maxilliped 2 (Fig. 4I).—Coxo-, basi-, and endopodite setation unchanged. Exopodite with 8 natatory setae.

Color.—Now appearing ocherous orange. Dorsal spine, abdomen, and telson darkest. Lateral spine with orange coloration on ventral surface. Orange chromatophores: at base of rostral spine, another midway to tip; on 2 or 3 basipodite of maxillipeds. Sixth somite and telson each with pair of orange-brown chromatophores medioventrally. Other chromatophore pattern remains as in first stage.

Fourth Zoea

Carapace length: 0.80 mm; 5 specimens examined.

Carapace (Fig. 5A).—Similar in form to third stage, elongate dorsal spine now with 5 setae on anterior margin as illustrated. Posterodorsal border now with 4 setae, posterolateral margin with 6. V-shaped process on ventrolateral margin less blunt than previous stages.

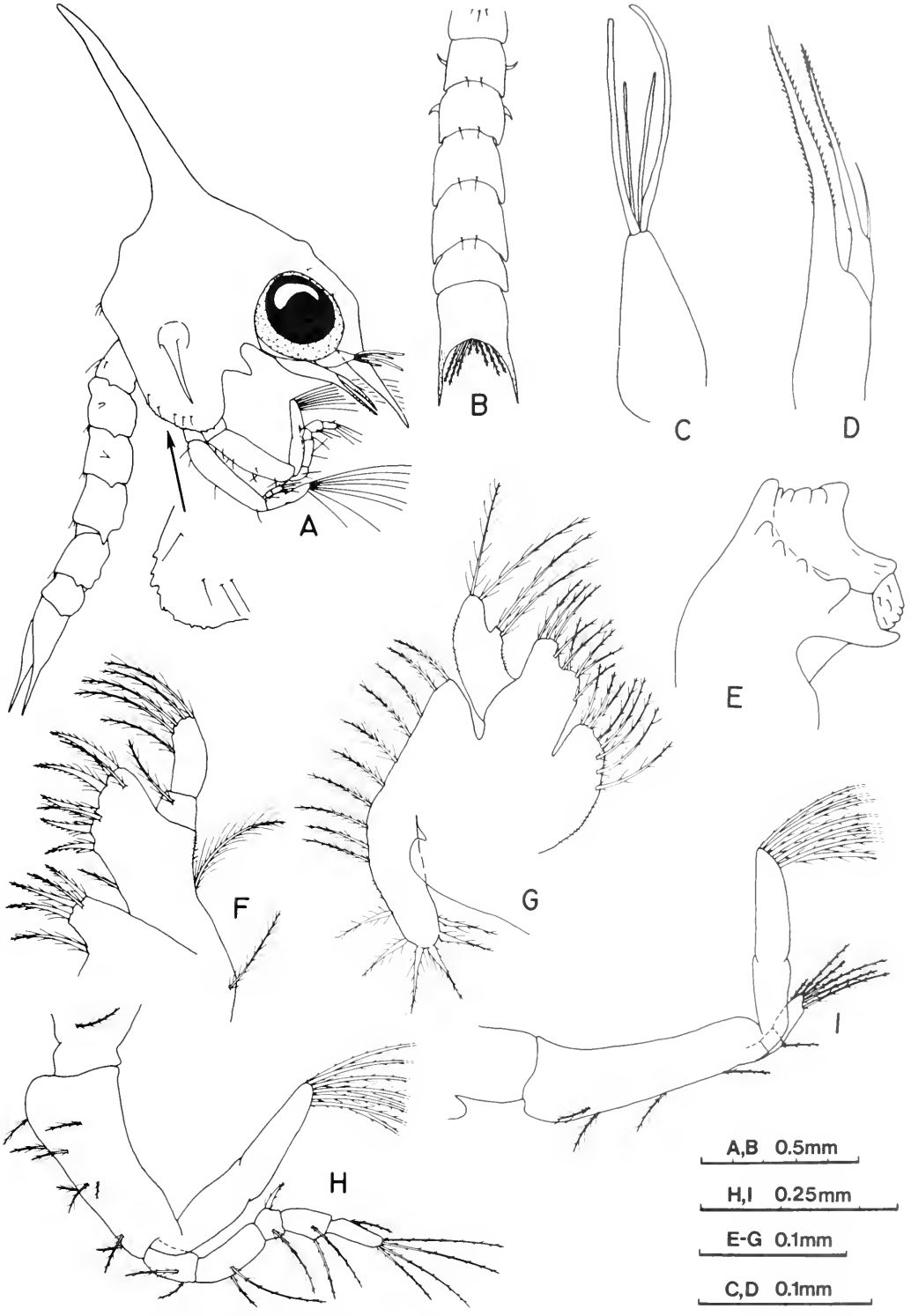

FIGURE 4.—Third zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandible; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

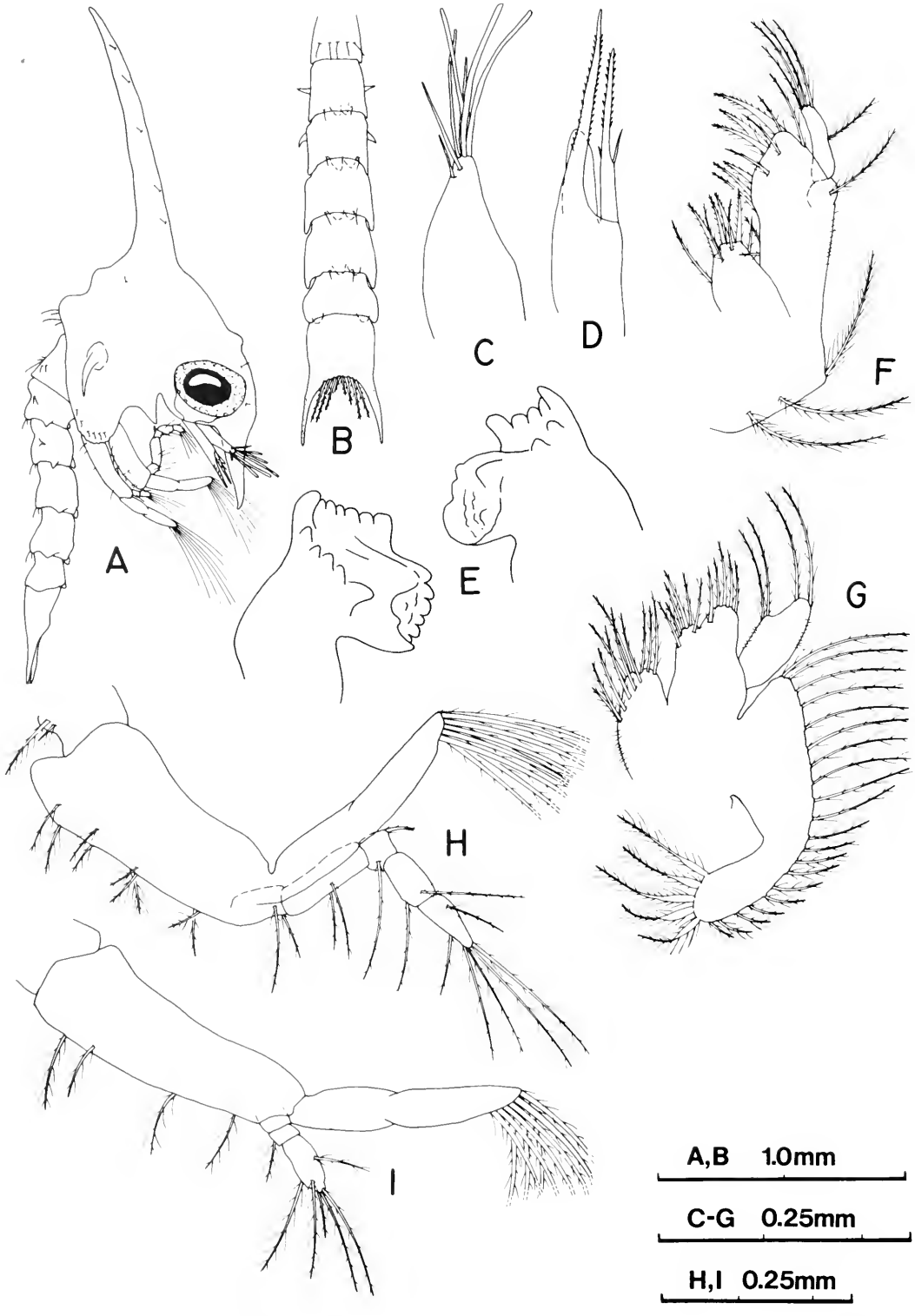

FIGURE 5.—Fourth zoeal stage of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C) antennule; (D) antenna; (E) mandibles; (F) maxillule; (G) maxilla; (H) maxilliped 1; (I) maxilliped 2.

Abdomen and Telson (Fig. 5B).—Pleopod and uropod buds now present on somites 2-5 and 6, respectively. First somite now with 5 middorsal setae.

Antennule (Fig. 5C).—Conical rod with 5 terminal plus 2 subterminal aesthetases.

Antenna (Fig. 5D).—Armature and form similar to previous stage. Endopodal bud now present, less than one-half length of protopodal process.

Mandible (Fig. 5E).—Similar to third stage with addition of 1 bluntly rounded tooth on posterior edge of incisor process.

Maxillule (Fig. 5F).—Endopodite setation unchanged, basal endite now with 11 or 12 setae, coxal endite with 8 setae, 3-5 plumose setae on basal margin, placed as illustrated.

Maxilla (Fig. 5G).—Setal formulae on endopodite 2,2; basal endites 6,5; coxal endites 7,3. Scaphognathite with 17-21 thinner setae, plus 5 or 6 stouter distal setae.

Maxilliped 1 (Fig. 5H).—Coxopodite now with 2 ventral setae. Basipodite setation unchanged. Endopodite now with 2,2,1 plus 1 spine, 2,5+I. Exopodal natatory setae 9.

Maxilliped 2 (Fig. 5I).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 9 natatory setae.

Color.—Ocherous orange; additional orange and brown chromatophores appear together as follows: 1 each posterior to eyestalks, 1 anteromedially on somites 2-4, a pair anteroventrally on somites 5 and 6, 1 anteroventral plus another medioventral pair on telson, and 1 each at base of lateral spine.

Fifth Zoea (Ultimate)

Carapace length: 1.2 mm; 3 specimens examined.

Carapace (Fig. 6A).—Similar to previous stage, dorsal spine elongate, posterodorsal border with 4 setae, posterolateral margin with 8 setae.

Abdomen and Telson (Fig. 6B).—First somite with 6 or 7 middorsal setae, all other morphological features similar to fourth stage. Pleopod buds elongate, all now with endopodites.

Antennule (Fig. 6E).—Endopodal bud present laterally below 2 tiers of aesthetascs, 5 unequal terminal aesthetases plus 1 seta, and 6 subterminal aesthetases. Basal region swollen, unsegmented.

Antenna (Fig. 6F).—Endopodal bud now three-fourths length of protopodal process. Exopodal spine remains shorter than protopodite.

Mandible (Fig. 6I).—Palp bud present on anterior surface. Incisor and molar form and armature as in fourth stage.

Maxillule (Fig. 6J).—Endopodal setation unchanged. Basal endite with 15 or 16 setae, coxal endite with 10-13 setae, 3 additionally on basal margin.

Maxilla (Fig. 6K).—Endopodite unchanged. Setae of basal endites 8,8, coxal endites 11,4. Scaphognathite with 31-33 marginal setae.

Maxilliped 1 (Fig. 6L).—Coxopodite now with 3 ventral setae. Basi- and endopodite setation unchanged. Exopodite now with 11 natatory setae.

Maxilliped 2 (Fig. 6M).—Coxo-, basi-, and endopodal setation unchanged. Exopodite now with 12 natatory setae.

Maxilliped 3 (Fig. 6N).—Rudimentary trilobed, unsegmented naked process.

Color.—Similar to previous stage. Numerous additional brown and orange chromatophores appear especially on anterior region of cephalothorax and sixth abdominal somite and telson. Tips of maxillipedal exopodites now with orange hue. On day before metamorphosis to megalopa, ultimate fifth stage zoea has very dark brown cephalothorax with innumerable spidery brown and orange chromatophores interspersed. Dorsal spine and abdomen vermilion. Coalesced orange and brown chromatophore occur posteriorly on the eyestalk.

Fifth Zoea (Penultimate)

Carapace length: 1.1 mm; 3 specimens examined.

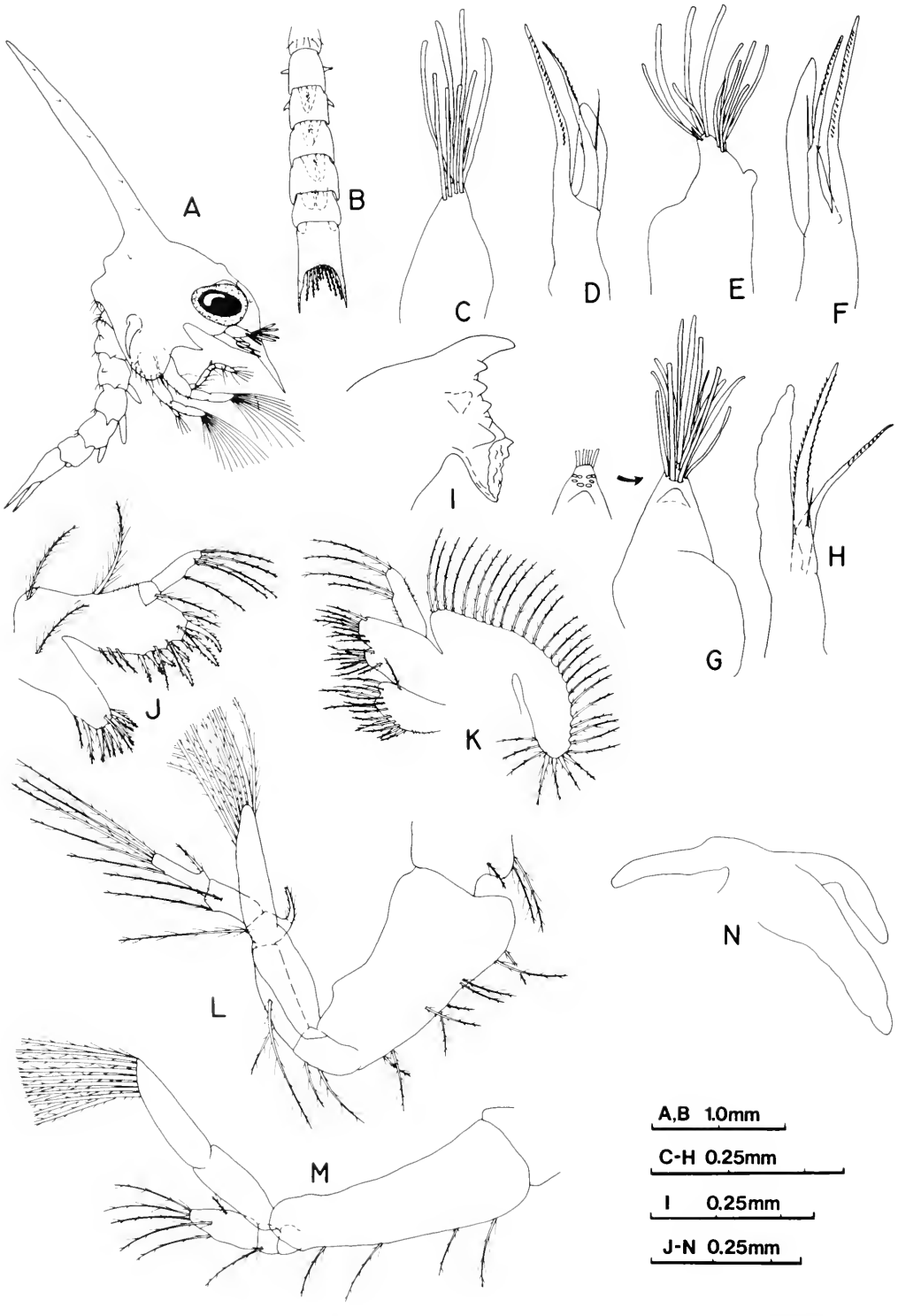

FIGURE 6.—Fifth (ultimate, A, B, E, F, I-M, penultimate, C, D) and sixth (G, H) zoeal stages of *Cyclograpsus integer*. (A) Lateral view; (B) abdomen and telson; (C, E, G) antennule; (D, F, H) antenna; (I) mandible; (J) maxillule; (K) maxilla; (L) maxilliped 1; (M) maxilliped 2; (N) maxilliped 3.

Remarks.—The penultimate fifth stage zoea molted to a sixth stage before metamorphosing to megalopa. Only morphological features differing significantly from the ultimate fifth stage, which molts directly to megalopa, are discussed below.

Antennule (Fig. 6C).—No endopodal bud present, 5 terminal plus 4 subterminal unequal aesthetascs present.

Antenna (Fig. 6D).—Endopodal bud only one-half length of protopodal process, other armature and processes similar.

Mandible.—No palp present, other armature similar.

Abdomen.—Pleopod buds without endopodites, less elongate and developed.

Sixth Zoea

Carapace length: 1.3 mm; 3 specimens examined.

Remarks.—The sixth stage zoea appear similar in form and armature to the ultimate fifth stage. Only morphological characters which may be used to distinguish between the two stages are discussed below.

Carapace.—Little inflated, posterodorsal border with 6 setae.

Abdomen and Telson.—First somite with 8 or 9 middorsal setae, pleopod buds more elongate.

Antennule (Fig. 6G).—Aesthetascs arranged in tiers as illustrated, progressing distally 2,2,4,4.

Antenna (Fig. 6H).—Endopodal bud obscurely segmented, five-sixth length of protopodal process.

Mandible.—Palp more elongate.

Maxillule.—Basal endite with 18 setae, coxal endite with 12 setae, basal margin with 3 or 4 plumose setae.

Maxilla.—Basal endites with 9,8, coxal with 12,4 setal formulae. Scaphognathite with 34-37 marginal setae.

Maxilliped 1.—Coxopodite with 4 or 5 ventral setae. Basipodite setal formulae variable from 9 to 11 ventral setae, exopodite with 12 or 13 natatory setae.

Maxilliped 2.—Coxopodite naked or with 1 seta ventrally, endopodite setation variable either 0,1,5+I or 1,1,5+I. Exopodite with 13 or 14 natatory setae.

Maxilliped 3.—Trilobed as in fifth stage, may have 1 seta on each lobe.

Color.—Similar to fifth stage, innumerable spidery brown and orange chromatophores, entire maxillipeds now orange brown.

Megalopa

Carapace length × width: 1.45 × 1.25 mm; 7 specimens examined.

Remarks.—Megalopae molting from both fifth and sixth zoeal stages are similar in form and armature. Morphological characters distinguishing megalopae, which molted from ZVI, are placed in brackets under the appropriate headings.

Carapace (Fig. 7A, B).—Cephalothorax subquadrate, laterally inflated. Smooth surface covered with hairs as illustrated, plus innumerable setae on posterior and posterolateral borders. Frontal region developed into ventrally deflexed, bluntly rounded rostrum with distinct median cleft, appearing as U-shaped sinus viewed dorsally. Anterolateral margins of carapace produced into 2 indistinctly rounded lobes. Eyes large, projecting laterally.

Abdomen and Telson (Fig. 7A, a, E-I).—Somites 1-5 with bluntly rounded posterolateral processes, somite 6 much broader than long; all with setae as illustrated; telson semicircular, no posterior marginal setae, 2 pairs medially, others as illustrated. Pleopods well developed, with variable setation 16-19, 20 or 21, 19-22, 22 [19-21, 21, 22, 22], all endopods with 3 hooked setae terminally. Uropods with 10 or 11 exopodal plus 1 protopodal seta [11 or 12 plus 1].

Pereopods (Fig. 7A, C, D).—Chelipeds well developed, somewhat inflated, unarmed, equal, shorter than walking legs, gape of chelae irregularly serrated, setae on remaining articles as

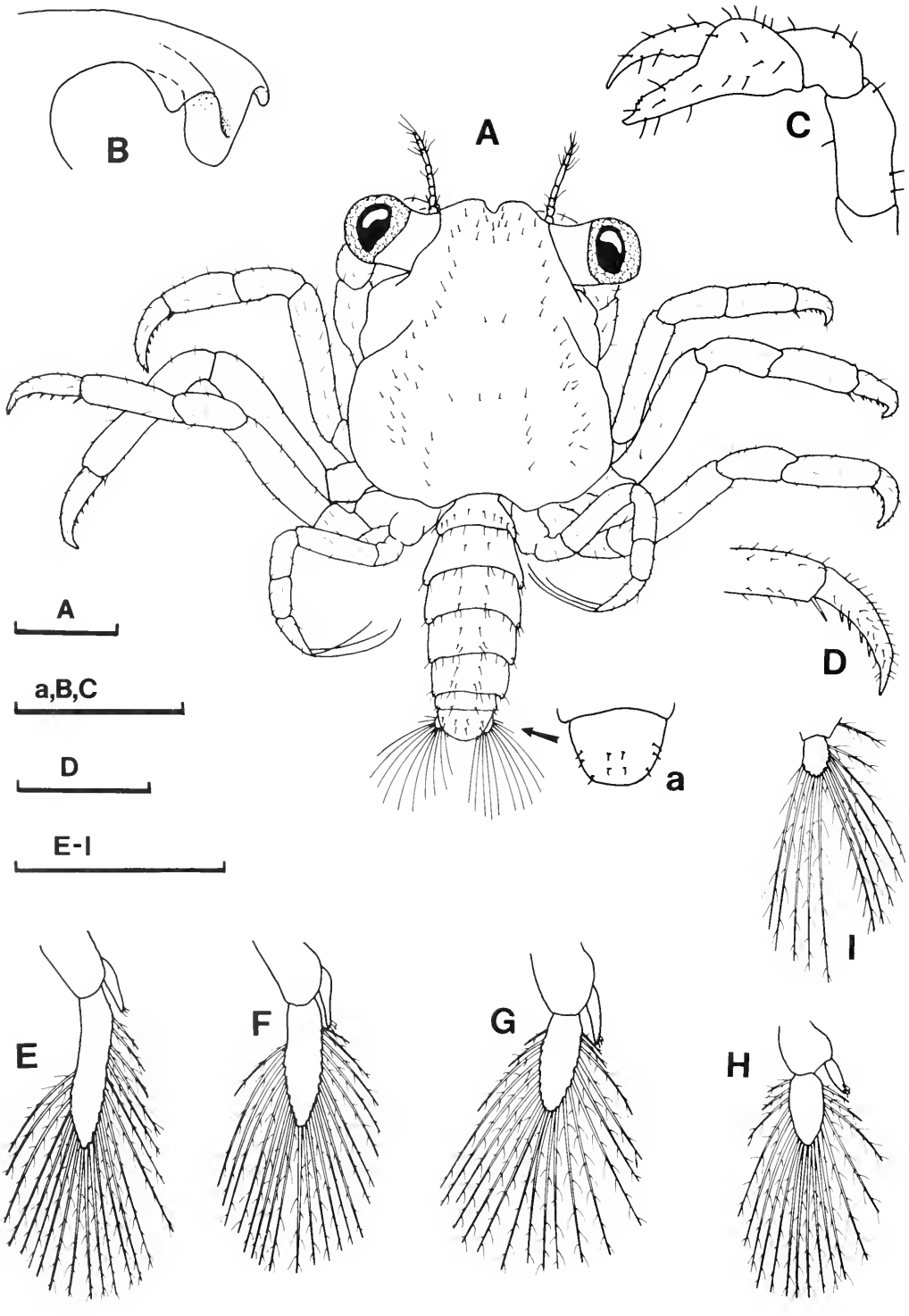

FIGURE 7.—Megalopa stage of *Cyclograpsus integer*. (A) Dorsal view; (a) telson; (B) rostrum (anterolateral view); (C) left cheliped; (D) second pereopod dactyl; (E) first pleopod; (F) second pleopod; (G) third pleopod; (H) fourth pleopod; (I) uropod. Scale lines = 0.5 mm.

illustrated. Second to fourth pereopods elongate, similar, each with distoventral tooth on propodus and 4 ventral teeth on dactyl. Fifth pereopod dactyl with 3 [3 or 4] long pectinate setae (= brachyuran feelers).

Antennule (Fig. 8A).—Biramous, peduncle 3-segmented, extremely enlarged, bulbous basal segment with 2 or 3 [3-5] setae, middle segment much smaller ovoid, with 2 or 3 [3 or 4] setae, distal segment larger than middle, expanded distally, naked. Flagellar lower ramus 1-segmented, 3 terminal, 1 subterminal setae; upper ramus 4-segmented, tiered aesthetascs usually arranged (0)(6), (6, plus 1 lateral seta), (5, plus 1 terminal seta).

Antenna (Fig. 8B).—Peduncle with 2-4 distal setae; flagella with setation 1,2,0,0,2-3, 0,5,3,3, [1,2,0,0,4,0,4-5,3,3-4].

Mandible (Fig. 8C).—Incisor process smooth, spatulate; molar process elongate, tubular; palp 2-segmented with 0,9 setae.

Maxillule (Fig. 8D).—Endopodite irregularly shaped, with 4 distal, 2 or 3 lateral setae; basal endite with 12 spines, 12-14 setae [25-29], coxal endite with 8 spines plus 2 rows of about 9 or 10 processes each [32] arranged in tiers as illustrated. Basal margin with 4 [3-5] long setae.

Maxilla (Fig. 8E).—Endopodite unsegmented, 2 [3] setae on lower lateral margin. Basal endites with 9-11, 12-14, [10-12, 13-16] processes, coxal endites with 7, 18-20 [8 or 9, 20-22] processes. Scaphognathite with 61-62 marginal setae plus 5 laterally on the blade as shown [70-72 plus 5].

Maxilliped 1 (Fig. 8F).—Exopodite 2-segmented, with 2 distal, 4 terminal setae. Endopodite irregularly shaped, unsegmented, 4-8 setae scattered over length. Basal endite with 13-17 [15-17], coxal endite with 17-20, setae. Epipodite with 9 or 10 [13-18] long, aesthetascoid processes.

Maxilliped 2 (Fig. 8G).—Exopodite 2-segmented, 2 lateral, 4 terminal setae. Endopodite 5-segmented setation progressing distally 3-7, 1, 1, 3 or 4, 6 or 7. Epipodite with 4-7 distal, 1 proximal, aesthetascoid processes, [9-11, plus 1]. Protopodite setae not determined.

Maxilliped 3 (Fig. 8H).—Exopodite 2-segmented with 5 or 6 proximal, 4 or 5 terminal setae; endopodite 5-segmented setae progressing distally 16-18, 12 or 13, 8-10, 10 or 11, 6 or 7 [18-20, 13, 8-12, 9-12, 8], protopodite with 21 or 22 [22-26] setae, epipodite with 21-26 aesthetascoid processes distally plus 8 or 9 setae proximally [30-32, plus 8-11].

Color.—Innumerable spidery orange and brown chromatophores completely covering cephalothorax, abdomen, pereopods, eyestalks, and all feeding appendages.

DISCUSSION

Zoeal Stages

The complete larval development of <20% of the known species of *Cyclograpsus* has been studied, and zoeal stages within the genus will be difficult to identify in the plankton. Larvae of the genus are unusual in several respects; therefore, some morphological and developmental characters may yet prove to be of aid in identification. For example, in at least two species (*C. integer* and *C. cinereus*) lateral carapace spines are lacking in the first stage, but appear in all later stages (Costlow and Fagetti 1967). Within the genus, some form of armature occurs on the ventrolateral carapace margin, either as spines, small teeth, setae, or a combination of these. In general, teeth or spines occur in the early stages and are replaced by setae as development proceeds. The number and time of appearance of these processes seems to be species specific (Table 2; and summary in Fagetti and Campodonico 1971). In addition to the ventrolateral processes, later larval stages of all species of *Cyclograpsus* studied to date bear some form of setation of spination on the posterior middorsal margin of the carapace above the insertion of the abdomen. In *C. cinereus*, this takes the form of paired spines in the second and subsequent zoeal stages (Costlow and Fagetti 1967); in *C. punctatus*, a similar situation appears in the third and later stages (Fagetti and Campodonico 1971), whereas in *C. integer*, 3 setae appear in the third and subsequent stages.

Unfortunately, the characters noted above are not restricted to *Cyclograpsus* but are shared, at least in part, among zoeae of several other genera in the four grapsid subfamilies. For instance, several genera in the Grapsinae, Varuninae, and Sesarminae have zoeal stages which lack lateral

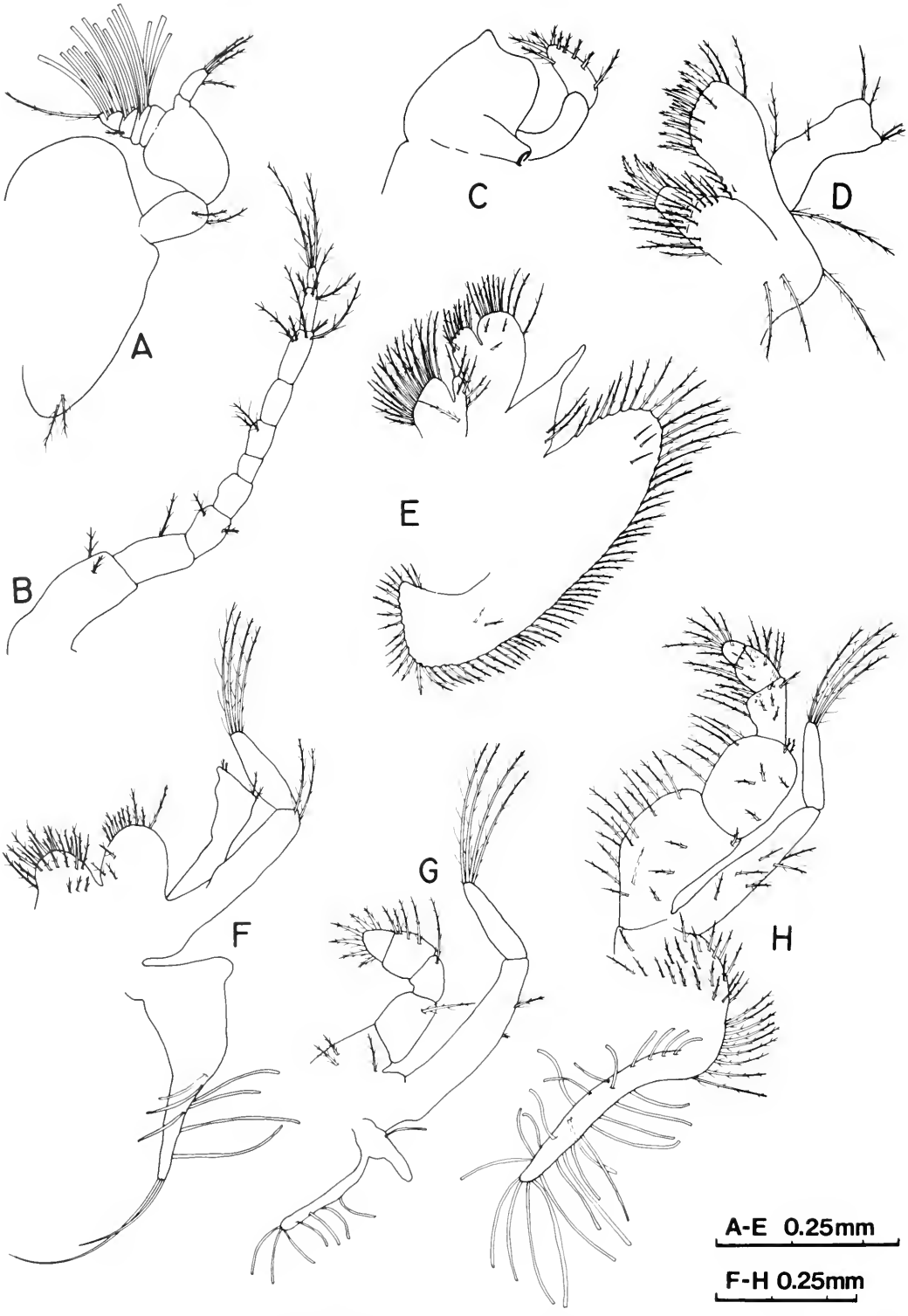

FIGURE 8.—Megalopa stage of *Cyclograpsus integer*. (A) Antennule; (B) antenna; (C) mandible; (D) maxillule; (E) maxilla; (F) maxilliped 1; (G) maxilliped 2; (H) maxilliped 3.

TABLE 2.—Comparison of selected zoeal characters in five species of *Cyclograpsus*.

Species	Carapace spines: Dorsal	Carapace spines: Lateral	Ventro-lateral	Appendages antennule	Antennae (exopod)	Maxilliped 1: Basipod	Maxilliped 1: Endopod	Maxilliped 2: Basipod	Maxilliped 2: Endopod	Abdomen/(telson) armature
C. cinereus (Costlow and Fagetti 1967)										
Zoea I	Gibbose	Absent	8 spines	2 aesth., 2 setae	Protopod 1.3× exopod (1 lat. spine)	[1]1,2,3,3	2,1,1,2,4+I	1,1,1,1	0,1,1+3+I	Somite 2 spined; (I+3)
Zoea II	Curved	Present	6 spines, 6 setae	4 aesth.	Protopod 1.5× exopod	[1]1,2,3,3	2,2,1,2,4+I	1,1,1,1	0,1,1+3+I	Somite 2 spined; (I+3)
Zoea III	Curved	Present	5 spines, 10 setae	4 aesth.	Protopod 1.5× exopod	[1]2,1,3,3	2,2,1+I,2,4+I	1,1,1,1	[1]0,1,2+3+I	Somite 2 spined; (I+4)
Zoea IV	Nearly straight	Present	4 spines, 14 setae	5+1 aesth.	Protopod 1.6× exopod (1.4× endopod)	[1]1,1,3,3	2,2,2,2,1+4+I	1,1,1,1	[1]0,1,2+3+I	Somite 1 with 5 dorsal spines
Zoea V	Straight	Present	10 spinules, 18 setae	5+4 aesth., 2 lateral setae	Protopod 1.8× exopod (0.7× endopod)	[1]4,2,3,2?	2,1+II,1+I, 1+I,1+4+I	1,1,1,1	0,1,1+3+II	Somite 1 with 5 dorsal spines
C. punctatus (Fagetti and Campodonico 1971)										
Zoea I	Curved	Present	12 spines	2 aesth., 2 setae	Protopod 1.25× exopod (2 lat. spines)	2,2,3,3	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 spined; (I+3)
Zoea II	Nearly straight	Present	2 setae	4 aesth.	Protopod 1.5× exopod	2,2,3,3	2,2,1,2,4+I	1,1,1,1	0,2,2+3+I	Somites 2,3 spined; (I+3)
Zoea III	Nearly straight	Present	11 setae	5 aesth	Protopod 1.4× exopod	2,2,3,3	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+4)
Zoea IV	Nearly straight	Present	12 setae	6+1 aesth.	Protopod 1.1× exopod (2.9× endopod)	2,2,3,3	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+4)
Zoea V	Nearly straight	Present	15 setae	4+4 aesth., 1 lateral	Protopod 1.23× exopod (1.4× endopod)	2,2,3,4	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somite 1 with 3 setae; (I+5)
C. integer										
Zoea I	Slightly curved	Absent	Irregularly dentate	4 aesth.	Protopod ≅ exopod (1 lat. seta)	2,2,3,2	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2-4 with knobs (I+3)
Zoea II	Slightly curved	Present	1 seta	6 aesth.	Protopod ≅ exopod (1 lat. seta)	2,2,3,2	2,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs
Zoea III	Nearly straight	Present	5 setae	4 aesth.	Protopod > exopod	2,2,3,2	2,2,1+I,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea IV	Sparsely setose	Present	6 setae	5+2 aesth.	Protopod 1.2× exopod (1.9× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea V (U)	Sparsely setose	Present	8 setae	5+6 aesth., 1 lateral seta	Protopod 1.07× exopod (1.18× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea V (P)	Sparsely setose	Present	8 setae	5+6 aesth	Protopod 1.05× exopod (1.75× endopod)	2,2,3,2	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+4)
Zoea VI	Sparsely setose	Present	8 setae	2,2,4,4 aesth	Protopod 1.18× exopod (= endopod)	9-11 setae (variable)	2,2,1+I,2, 1+4+I	1,1,1,1	0,1,2+3+I or 1,1,2+3+I	Somites 2,3 with knobs (I+4)
C. lavauxi (Wear 1970)										
Zoea I	Slightly sigmoid	Present	ca 7 setae	3 aesth.	Protopod 1.3× exopod (3 lat setae)	[1]2+1,1,1,1	1,2,1,2,4+I	1,1,1,1	0,1,2+3+I	Somites 2,3 with knobs (I+3)
C. insularum (Wear 1970)										
Zoea I	Slightly curved	Present	ca 20 small teeth	4 aesth.	Protopod 1.5× exopod (3 lat setae)	3,3,3,3	2,2,1,2,4+I	1,1,1,1	0,2,2+3+I	Somites 2-4 spined; (I+3)

[1]Data interpolated from illustrations.

carapace spines. No first stage grapsine zoeae, no *Sesarma* (Sesarminae), nor *Acmaeopleura* (or possible *Gaetice*) larvae in the Varuninae have these spines (see summary in Wilson 1980). Moreover, *Pachygrapsus* zoeae (Grapsinae), like some larvae in *Cyclograpsus*, apparently lack lateral spines in the first, but possess these in subsequent, zoeal stages (Schlotterbeck 1976; Bourdillon-Casanova 1960). On the other hand, all known plagusiine larvae have lateral spines from the first stage onward (Wilson 1980).

Setation or spination on the ventrolateral carapace margin is another widely shared feature among grapsid genera. Examples include *Brachynotus* (Bourdillon-Casanova 1960), *Hemigrapsus* (Kurata 1968), and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979) in the Varuninae, *Sesarma* (Baba and Miyata 1971) in the Sesarminae, *Leptograpsus* (Wear 1970) in the Grapsinae, and *Plagusia* (Wilson and Gore 1980) in the Plagusiinae. In many instances, however, carapace and telson spine formulae differ substantially from that seen in larvae of *Cyclograpsus*, thereby allowing at least provisional separation among these zoeae.

Regarding middorsal carapace setation, many descriptions of brachyuran larvae either fail to note its occurrence or do not allow judgment to be made because of undetailed illustrations. A general perusal of the literature available on grapsid larvae (Wilson 1980) shows that, in addition to *Cyclograpsus*, only a few sesarmine genera had this feature indicated, including *Chasmagnathus* (Boschi et al. 1967), *Helice* (Baba and Moriyama 1972), and in the Varuninae *Hemigrapsus* (Hart 1935) and *Cyrtograpsus* (Scelzo and Lichtschein de Bastida 1979). Several other studies provide suitably detailed illustrations which suggest that this character may be more or less widespread among the zoeae of these subfamilies. However, these setae are apparently absent in plagusiine and grapsine larvae, as far as can be ascertained from the literature. Because these setae usually do not appear until later zoeal stages (ZIII and beyond) their usefulness as an identifying character is somewhat limited.

One other carapace feature that seems noteworthy, at least for the genus *Cyclograpsus*, is the pterygostomian region of *C. integer*; this region is produced into a triangular, toothlike prominence in the first stage, which becomes more sharply pronounced as development proceeds. In *C. cinereus*, this prominence is always bluntly rounded until the last stage, when it becomes more acute. In *C. punctatus* the prominence develops very slowly and apparently never becomes acute. Only the first zoeal stages are known in *C. lavauxi* and *C. insularum* (Wear 1970) and the prominence is not well developed in either, being similar to that seen in *C. punctatus*. Although the toothlike prominence is seen to some extent in other grapsid zoeae, it does not appear to be quite as prominent, based on the illustrations provided in several studies.

The type of antenna has always been considered an important classification feature in brachyuran larvae (Aikawa 1929). Most brachyuran larvae have a type B antenna (i.e., exopod about 0.5-0.75× the length of the protopodal spine). This type is widely present throughout the Grapsidae, being found predominantly in the Sesarminae and Varuninae, but seen in only isolated instances in either the Grapsinae or Plagusiinae. Nearly all Grapsinae have a type C antenna (exopod substantially reduced in size to the protopodal spine), an advanced character also shared for the most part among the known larvae of plagusiine genera (see summary in Wilson 1980).

All *Cyclograpsus* larvae possess a type B antenna, with the exception of *C. integer*, which has a type A antenna (exopod and protopod about equal). The type A antenna is considered to be primitive (Aikawa 1929). The larvae of *C. integer* are even more remarkable in having the antennal protopodal spine and exopod both armed along their respective lengths with rows of teeth, in a manner similar to that seen in *Eriocheir* zoeae (Varuninae; Aikawa 1929), and reminiscent of some antennae exhibited by larvae in several xanthid genera (e.g., Scotto 1979). In other *Cyclograpsus* zoeae, the exopod is entire, and only the protopodal spine is so armed. *Cyclograpsus integer* is thus noteworthy for two exceptions: 1) an antenna of a form (i.e., doubly armed) rarely noted within the Grapsidae, and 2) an antenna type (A) found in no other zoeae of any genus in the Grapsidae.

Rice (1980) summarized the available knowledge on the Grapsidae in a major paper dealing with brachyuran zoeal classification. In attempting to delineate useful features among the four subfamilies of grapsid crabs, he suggested that the known zoeae of the Varuninae and Sesarminae might be distinguished from the Grapsinae and Plagusiinae by always having a well-developed antennal exopod at least half as long as the

spinous (protopodal) process (i.e., type B) and bearing at least 10 medial setae on the basis of the first maxilliped. Wilson (1980) subsequently demonstrated that *Euchirograpsus* larvae (Varuninae) have extremely shortened antennal exopods (type C) plus only 8 basipodal setae, and therefore are more allied to Grapsinae and Plagusiinae larvae than to those of the Sesarminae or other Varuninae. As noted above, *C. integer* also refute Rice's suggestion in regard to the Sesarminae, by having a type A antenna and by bearing 9 (instead of 10) basipodal setae. Larvae of *C. cinereus* also have 9 basipodal setae on maxilliped 1, but these occur in a grouping different from that seen in *C. integer*; *C. lavauxi* larvae have 6 and *C. insularum* have 12 setae (Table 2).

As to other features for distinguishing among the larvae of *Cyclograpsus*, setation and armature of abdominal somites can be useful. Beginning with the second (*C. integer*), third (*C. cinereus*), or fourth zoeal stage (*C. punctatus*), nonpaired, usually elongate or spinelike setae are found on the posterodorsal margin of the first abdominal somite. As development proceeds these setae either increase in number (1, 3, 5, in *C. integer* stages), or remain unchanged (3, *C. punctatus*; 5, *C. cinereus*). Somite armature shows similar diversity, with a hooklike spine or knob on the second (*C. cinereus*), second and third (*C. punctatus*, *C. lavauxi*), or second through fourth somites (*C. integer*, *C. insularum* first zoea). Regrettably, neither of these characters are specific for *Cyclograpsus* larvae because they occur in other brachyuran zoeae and are seen, for example, in the Goneplacidae (*Carcinoplax*, Lee and Hong 1970; *Tritodynamia*, Boucquet 1965), as well as several other families less closely related to the Grapsidae (Lebour 1928, fig. 5, p. 483).

The telsons in *Cyclograpsus* zoeae all seem referrable to Aikawa's (1929) type B (i.e., without supernumerary lateral spines, and typically brachyuran in shape). The telson formula of I+3 (= furcal spine, plus movable spiny seta; Gore 1979) changes in stage III to I+4 in *C. integer*, *C. cinereus*, and *C. punctatus*; the latter species, however, adds an additional medial pair of setae in stage V, becoming I+5. Table 2 provides a summary of all of these features.

Megalopal Stage

The megalopae of the three *Cyclograpsus* species in which complete development is known differ substantially from one another and should prove more easily separable than their respective larvae. The frontal region bears a strongly deflexed rostral spine in *C. punctatus* (Fagetti and Campodonico 1971), has a ventrally deflexed, bluntly rounded rostrum with a median cleft in *C. integer*, and is only slightly produced and without a rostral spine in *C. cinereus* (Costlow and Fagetti 1967). Other easily observed characters not requiring dissection include terminal setation on the telson, aesthetases on the antennule, exopodal setae of the third maxillipeds, pleopods, and uropods. These, plus characters requiring some dissection to observe, are summarized in Table 3.

None of the megalopal stages in any of the three species considered resembles the juvenile or adult crabs. Moreover, they do not exhibit easily noticeable differences from many other brachyuran megalopae, let alone grapsid megalopae. In general, lack of rostral spines, or with the rostrum only poorly developed, usually deflexed, and unarmed, is seen in many grapsid postlarvae. Many of the species have the lower ramus of the antennule appearing as a 1-segmented, simple, palplike process (as in *Chasmagnathus*, *Helice*, *Cyrtograpsus*, and others, Costlow and Fagetti 1967), or even reduced to a simple seta (*Sesarma*; Costlow and Bookhout 1962). But because of the paucity of descriptions there is little use in attempting further classification at this time.

In the discussion above we have demonstrated that several suggestions proposed by Rice (1980) for classifying grapsid larvae can no longer be considered useful. Although the distinctions among the larvae of the subfamilies Grapsinae and Varuninae, and Varuninae and Sesarminae have become blurred, we nonetheless reiterate the value of Rice's classification attempt, and draw special attention to his key to the brachyuran families based on zoeal characters. By using the characters he proposed, one may still arrive within the Grapsidae using the key, provided that the subfamilial headings are disregarded. Rice's couplet 26 may then be modified to read as follows:

26. Carapace without lateral spines in *all zoeal stages* 27
    Carapace *usually* with lateral spines *in all zoeal stages or without only* in first zoeal stage 28

TABLE 3.—Comparison of selected megalopal characters in three species of *Cyclograpsus*.

	C. integer	*C. cinereus*	*C. punctatus*
Cephalothorax	Numerous hairs dorsally	Dorsally naked[1]	Dorsally naked[1]
Front	Bluntly rounded, ventrally deflexed medially cleft rostrum	Slightly produced, without rostral spine	Strongly deflexed rostral spine
Telson processes	0 terminal, 3 lateral, 2 pairs dorsally	3 terminal, 3 lateral, 2 pairs dorsally	9 terminal, 8 dorsal (6 transversely)
Antennular aesthetascs	(0)(6)(6,+1 seta) (5,+1 seta)	(0)(3)(4,+1 seta)(5)	(0)(4)(4,+2 setae) (4,+3 setae)
Antennal flagella	9 articles	11 articles	9 articles
Mandibular palp	0,9 setae	0,9 setae	0,7 setae
Maxillule			
Basipod	24-26 processes [25-29]	21 processes	ca. 24 processes
Coxopod	28-30 processes [32]	11 processes	16 processes
Basal margin	4 setae [3-5]	No data	2 setae
Maxilla			
Endopod	0, +2 lateral setae	2, +1 lateral setae	1, 1+4 lateral setae
Scaphognathite	61-62 marginal setae [70-72]	ca. 70 marginal setae	ca. 65 marginal setae
Maxilliped 3			
Exopod	5-6 proximal, 4-5 distal setae	3 proximal, 5 distal setae[1]	2 proximal, 5 distal setae[1]
Pleopods			
Exopod setae	16-22 [19-22]	17-20	15-16
Uropod setae	1 protopodal, 10-11 exopodal [11-12]	1 protopodal, 10 exopodal	1 protopodal, 8 exopodal

[1]Data interpolated from illustrations; no specific description given [ ] = megalopal stage obtained from zoeal stage VI.

We look to future studies that will provide descriptions of several common genera in the Grapsinae (e.g., *Geograpsus*, *Goniopsis*), Sesarminae (*Metapograpsus*), as well as to additional studies on larvae of previously known genera in the Plagusiinae (*Plagusia*, *Percnon*), and Varuninae (*Euchirograpsus*, *Cyrtograpsus*, and the as yet unknown zoeae of *Glyptograpsus*). All have the potential for providing further clarification of relationships among the Grapsidae.

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REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE LONGSPINE PORGY, *STENOTOMUS CAPRINUS*[1, 2]

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ABSTRACT

Stenotomus caprinus mature at 90-125 mm TL as they approach age 1. Spawning occurs once a year in a discrete period of 50-80 days duration from January through April with peak activity in February or March. The male-female sex ratio was 1:1.21 in the spawning period. Spawning occurs in waters deeper than 27 m, and its timing coincides with the periodicity of onshore surface currents in the northern Gulf of Mexico. These currents probably transport eggs and larvae inshore to nursery areas <27 m deep where recruitment occurs. Young-of-the-year gradually disperse as they mature to waters 36-55 m deep where age I and II fish are most abundant. *Stenotomus caprinus* are most vulnerable to trawling at night. Growth in length is fastest in their first 8 months but slows greatly as they mature and divert energy towards reproduction. *Stenotomus caprinus* averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Maximum size is about 200 mm TL and maximum lifespan typically is 2.5-3 years. Total annual mortality rate is 83-99%, but postspawning survival, mortality rates, and lifespan vary greatly between year classes. Total weight-total length, length-length, and girth-total length relationships are presented. The population dynamics of *S. caprinus* appear quite different from those of *S. chrysops*, and the genus *Stenotomus* may show zoogeographic change at Cape Hatteras, N.C.

Stenotomus caprinus, the longspine porgy, ranges in the Gulf of Mexico (Gulf) from Campeche Bank, Mexico, to Apalachee Bay, Fla., (Caldwell 1955) and occurs rarely in the Atlantic to North Carolina (Dawson[5]). It is very abundant at depths of 40-110 m and is the dominant fish in the brown shrimp community (Hildebrand 1954; Chittenden and McEachran 1976; Chittenden and Moore 1977). *Stenotomus caprinus* makes up a significant portion of the catch in the industrial fishery of the north central Gulf (Roithmayr 1965; Gutherz et al. 1975).

Despite its abundance, little is known about this species. Its life history is known from general faunal studies such as Miller (1965), Moore et al. (1970), and Franks et al. (1972), although Henwood et al. (1978) described its food habits. Only Caldwell (1955), Henwood (1975), Henwood et al. (1978), and Dawson (footnote 5) have made studies specifically directed at *S. caprinus*.

This paper describes maturation and spawning seasonality, movements and spawning areas, growth and sizes at age, mortality and lifespan, merits of age determination by scales and length-frequency analysis, length-length, total weight-total length, and girth-total length relationships for *S. caprinus*.

METHODS AND MATERIALS

Stenotomus caprinus were collected monthly along a transect in the Gulf off Freeport, Tex., (Fig. 1) from October 1977 through March 1980 aboard a chartered shrimp trawler using double rigged 10.4 m shrimp trawls with 4.4 cm stretched cod end mesh and a tickler chain. Stations were occupied at depths of 5, 9, 13, 14, 16, 22, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m. Collections were made during the day through September 1978; thereafter, a day and night cruise were usually made each month. The 22 m depth range was primarily occupied after October 1978, and depths >47 m were first occupied in June 1979. Two tows of 10 min bottom time were made at each depth except that 1 tow was made prior to October 1978, 8-12 tows were made at 14 m, and 24 tows usually were made at 22 m.

All *S. caprinus* were separated from the catch, measured for total length, fixed in 10% Forma-

[1]Based on a thesis submitted by the senior author in partial fulfillment for the M.S. degree, Texas A&M University.

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[5]Dawson, R. A systematic revision of the sparid genus *Stenotomus*. M.S. Thesis in prep., The College of Charleston, Charleston, S.C.

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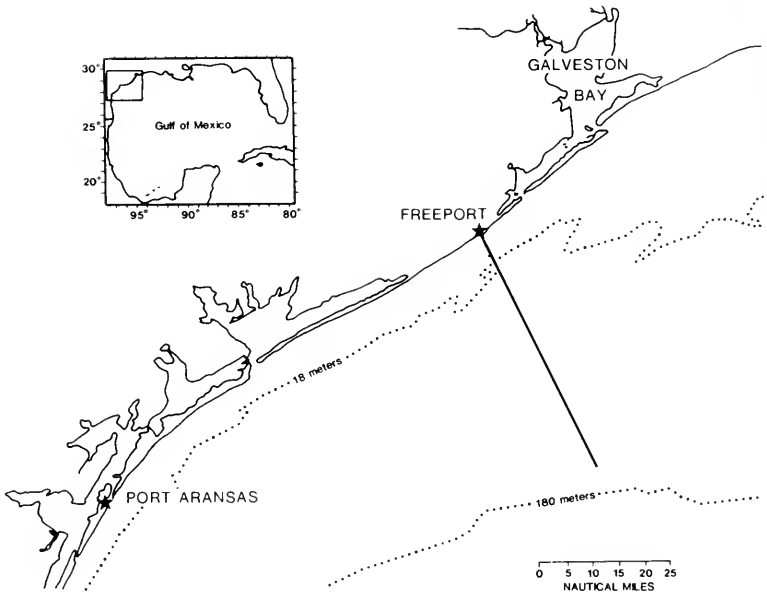


FIGURE 1.—Location of sampling areas with transect indicating stations occupied off Freeport, Tex.

lin,[6] and later preserved in 70% ethanol. For the period October 1978 to March 1980, 300 fish each month were selected by stratified random sampling to determine total length (TL), fork length (FL), standard length (SL), girth (G) at the fourth dorsal spine, total weight (TW), and ovary maturity stage and to take scale samples, except that only total weight, total length, sex, gonad weight, and ovary maturity stage were determined from October 1979 to March 1980. Female and immature fish were assigned gonad maturity stages (Table 1) similar to Kesteven's system (Bagenal and Braum 1971). Scales were taken below the lateral line near the tip of the pectoral fin following procedures for *S. chrysops* (Dery and Rearden[7]), and cellulose acetate impressions were examined using a scale projector.

Supplemental collections were made aboard the FRS *Oregon II* (NMFS) from 10 April to 1 May 1980 in the north central Gulf at depths of 9-91 m between long. 91°31′ and 92°00′W (Rohr et al.[8]). *Stenotomus caprinus* were selected from the catch without randomization procedures and measured in fork length.

TABLE 1.—Description of gonad maturity stages assigned to *Stenotomus caprinus*.

Stage	Description
1 Immature	Gonads barely or not visible.
2 Maturing virgin	Gonads very small, sexes not distinguishable.
3 Early developing	Sexes distinguishable but individual eggs are not visible.
4 Late developing	Eggs opaque, ovaries extending along <90% of gut cavity.
5 Gravid	Ovaries extend along 90% or more of lateral wall of gut cavity, < 50% of eggs translucent.
6 Ripe	Ovaries extend 90% or more of lateral wall of gut cavity, >50% of eggs translucent.
7 Spent/resting	Ovaries barely extend along lateral wall of gut cavity, flaccid with few small eggs. Similar in appearance to Stage 3, but occurs in fish large enough to have already spawned.

Year class identities were indicated by specifying the years in which the fish hatched. Age was determined by analysis of length frequencies, e.g., the Petersen method (Lagler 1956; Tesch 1971). The superior merits of this procedure for *S. caprinus* are noted in the section on Age Determination Using Scales. Size descriptions for each year class and each cruise (Table 2, Fig. 2) were based on major portions of frequency distributions cited. Boundaries between groups are indicated in Table 2 and Figure 2; mortality and growth calculations were based on groups defined by these boundaries. Arithmetic means were used to describe central tendencies for each year class and each cruise because length frequencies within year classes were

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

[7]Dery, L., and C. Reardon. 1979. Report of the State-Federal scup (*Stenotomus chrysops*) age and growth workshop. Woods Hole Lab. Ref. 79-57, 10 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[8]Rohr, B. A., A J. Kemmerer, and W. H. Fox, Jr. 1980. FRS *Oregon II* Cruise 106 4/10-5/1/80. Cruise Report, 12 p. Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567.

approximately normally distributed. Hatching dates of 15 February and 15 March were assigned to the 1978 and 1979 year classes, respectively, to estimate their growth and ages. Descriptions of spawning periodicity and growth assume that *S. caprinus* reach 20-30 mm TL 1-2 mo after hatching. This assumption and assigned hatching dates seem reasonable because: 1) *Stenotomus caprinus* average 13-14 mm TL/30 d growth during their first 8 mo of life (Fig. 3); 2) the slope and elevation of the regression of ovary weight on total length for the 1979 year class was greatest in mid-March (Fig. 4, Table 3) and back calculated length of this year class was −5.26 mm TL at 0 d of age (Fig. 5). A hatching date of 15 February was assigned to the 1978 year class because this year class recruited about 1 mo earlier in 1978, although gonad data are lacking for this period. There appears to be no published data on size at early age other than our findings.

Our interpretations of the life history of *S. caprinus* obviously apply best to the area off Freeport, Tex., but they probably apply to much broader areas in the Gulf, judging from the agreement of our findings with the general published data on this species.

MATURATION AND SPAWNING SEASONALITY

Results

Stenotomus caprinus mature at 90-125 mm TL as they approach age I. Sex could be determined by eye at 90 mm TL as many fish entered the Early Developing stage (Fig. 6). Fish entered the Late Developing, Ripe, and Gravid stages at 100-125 mm TL. These data are supported by the extrapolated x-intercepts of ovary weight on total length which were 80-100 mm TL during the January-April spawning period (Fig. 4, Table 3). Our estimates of size at maturity agree with the mean sizes at age I given later.

Little somatic growth occurs after *S. caprinus* enters the later stages of gonad maturation (Fig. 6). Mean sizes of fish approaching age I were 110 mm TL in the Early Developing, 113 mm in the Late Developing, 115 mm in the Gravid and Ripe, and 118 mm in the Spent/Resting stages.

Stenotomus caprinus spawn once a year in a discrete period from January through April. This period is indicated by collections off Texas of fish that were 30-40 mm TL in April 1978, 20-50 mm in May 1979, and 20-40 mm in February-March 1980 (Fig. 2), and by the capture of fish 20-80 mm TL in late April 1980 in the north central Gulf (Fig. 7). No spawning occurs from May through December, because the smallest fish collected in that period belong to year classes hatched before May. Peak spawning occurred in March and early April in 1979 and from January through March 1980 as indicated by the increased slopes and elevated ovary weight-total length regression lines in those periods (Fig. 4, Table 3). The sharply defined and readily followed length-frequency modes for each year class indicate that spawning occurs in one discrete period each year.

Gonad maturity data support a January-April spawning period and indicate that virtually all *S. caprinus* spawn at 12 mo of age. Fish in Gravid or Ripe stages occurred only in the period January-April, and Spent/Resting stage fish appeared immediately thereafter (Fig. 8). Virtually all spawning occurs in the period January-April and few fish delay spawning until age II because extremely few fish were in the Immature, Maturing Virgin, or Early Developing stages in that period.

The spawning period probably spans about 50-80 d within the January-April interval, assuming larger fish were spawned before smaller ones, and all fish grew at the same rate as noted later. The spawning period duration was approximated from growth increments and size ranges (expressed as 99% confidence limits for observations) of the 1978 and 1979 year classes in June and July (Table 2), their first months of full recruitment. The mean 99% confidence limit for observations in the June-July period was 22.19 mm in 1978 and 40.27 mm in 1979, and respective mean daily growth was 0.45 mm/d and 0.50 mm/d. Calculated lengths of spawning periods were 49 d in 1978 (22.19 mm ÷ 0.45 mm/d) and 82 d in 1979 (40.85 mm ÷ 0.50 mm/d). These estimates suggest that the successful spawning period is much shorter than the January-April interval indicated by length compositions and gonad data.

Stenotomus caprinus exhibited a sex ratio of 1.00 male to 1.21 females. This ratio was observed in 1,506 fish examined during the spawning period and differs significantly from 1:1 ($\chi^2 = 13.01$, $\alpha = 0.05$, df = 1).

Discussion

Our findings agree with the limited literature on *Stenotomus* reproduction. Previous workers

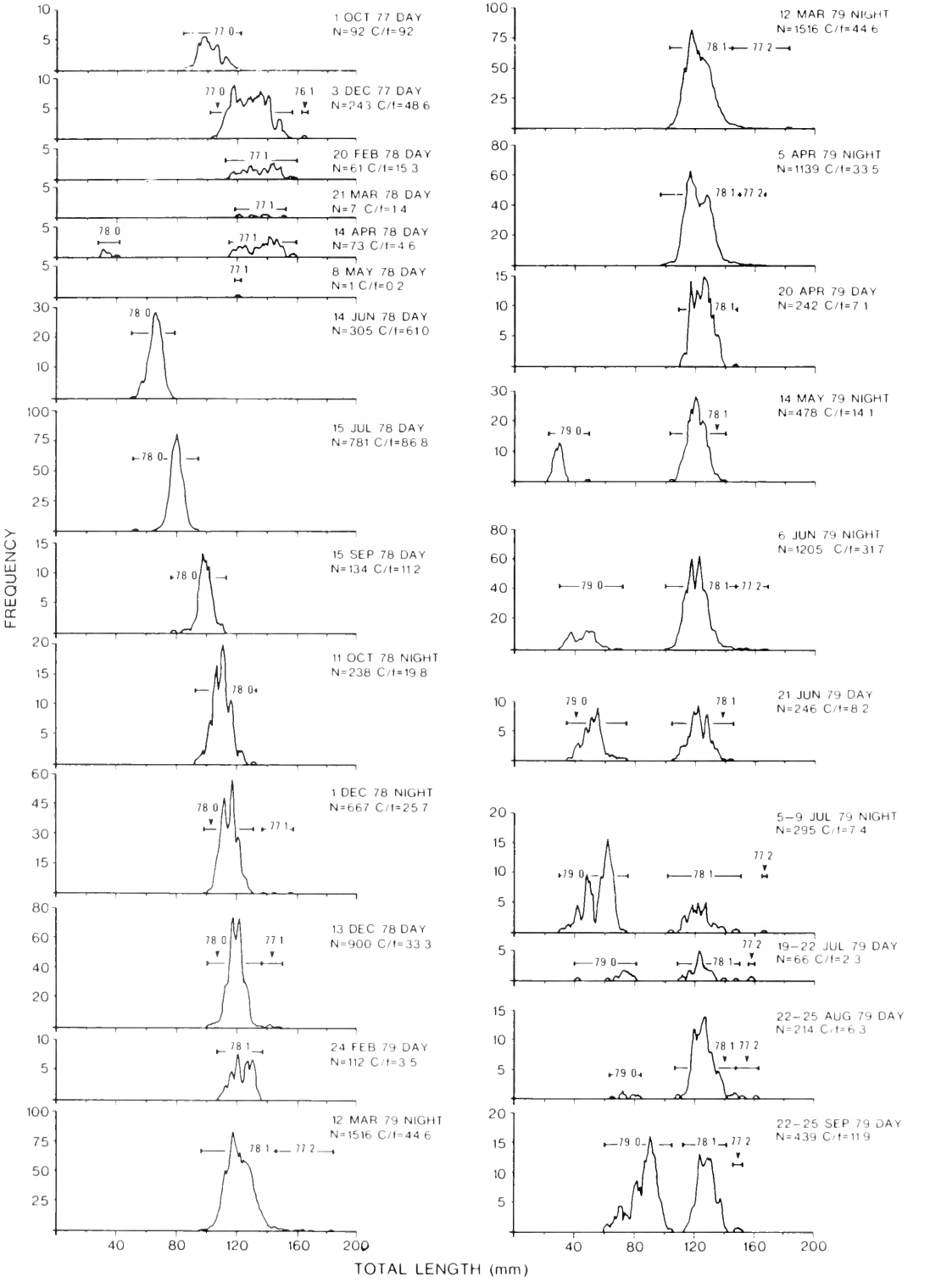
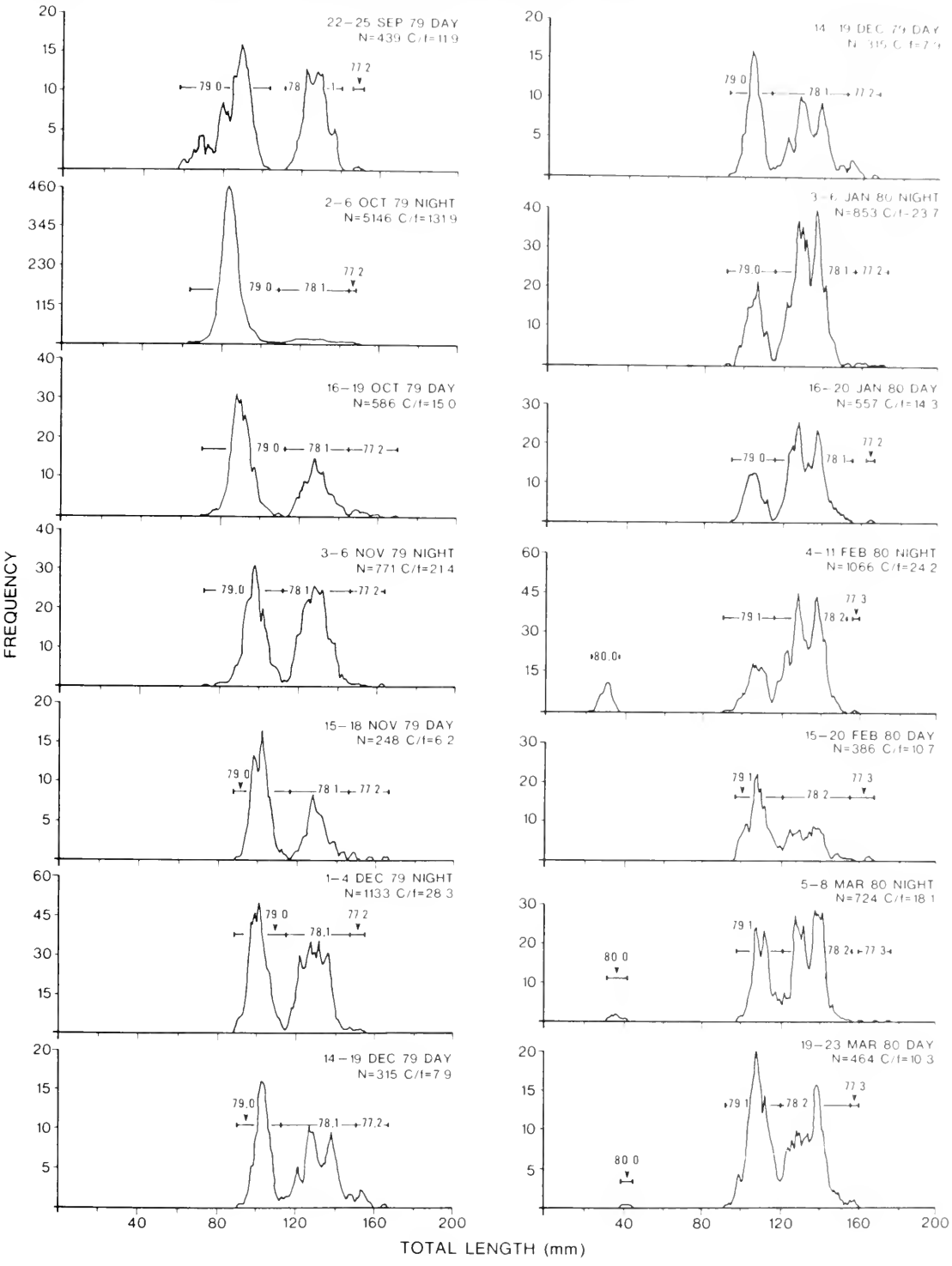


FIGURE 2.— Monthly length frequencies (moving averages of three) of *Stenotomus caprinus* off Freeport, Tex. Bars in each panel



indicate the size range of a year class. The first two digits within a bar indicate the year class; the last digit is age in years; e.g., 78.1 represents the 1978 year class when age I. C/f indicates number of individuals per 10-min tow.

TABLE 2.—Growth data (mm TL) for *Stenotomus caprinus* from the Gulf off Freeport, Tex. Increments with an asterisk (*) were adjusted to growth per 30 d and plotted in Figure 3. Night and day cruises are indicated by N and D. Observed size ranges delineate year class boundaries used in growth and mortality calculations.

Collection date	n	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1977 Year Class				
1 Oct. 1977, D	92	85-120	100.5	54.1	99.0-102.0	81.3-119.4	
5 Nov. 1977, D	0	—	—	—	—	—	—
3 Dec. 1977, D	242	103-157	127.6	123.3	126.2-129.0	99.0-156.2	+27.1
20 Feb. 1978, D	61	113-157	134.4	125.0	131.6-137.2	105.6-163.2	+6.8
21 Mar. 1978, D	7	119-150	132.0	116.0	122.4-141.6	94.3-169.7	−2.4
14 Apr. 1978, D	66	95-157	135.9	115.2	133.3-138.5	108.3-163.5	+3.9
8 May 1978, D	1	120	120.0	0	120.0	120.0	−15.9
14 June 1978, D	0	—	—	—	—	—	
15 July 1978, D	0	—	—	—	—	—	
15 Sept. 1978, D	0	—	—	—	—	—	
11 Oct. 1978, N	0	—	—	—	—	—	
1 Dec. 1978, N	3	136-155	145.3	82.3	128.6-162.0	92.3-198.3	+25.3
13 Dec. 1978, D	12	136-147	141.2	11.1	139.1-143.3	131.0-151.4	−4.1
24 Feb. 1979, D	0	—	—	—	—	—	
12 Mar. 1979, N	15	146-182	155.8	99.2	150.3-161.3	126.4-185.2	+14.6
5 Apr. 1979, N	7	151-165	156.4	22.3	152.2-160.6	139.9-172.9	+0.6
20 Apr. 1979, D	0	—	—	—	—	—	
14 May 1979, N	0	—	—	—	—	—	
6 June 1979, N	10	145-166	154.6	40.9	150.1-159.1	134.3-174.9	−1.8
21 June 1979, D	0	—	—	—	—	—	
5 July 1979, N	1	165	165.0	0	165.0	165.0	+11.4
19 July 1979, D	3	145-157	153.0	37.0	141.8-164.2	117.5-188.5	−12.0
22 Aug. 1979, D	3	146-159	151.7	44.3	139.5-163.9	112.8-190.6	−1.3
22 Sept. 1979, D	2	146-148	147.0	2.0	110.1-183.9	133.1-160.9	−4.7
2 Oct. 1979, N	4	145-160	153.0	38.7	144.4-161.6	124.4-181.6	+6.0
16 Oct. 1979, D	19	145-167	151.7	34.3	148.9-154.5	134.9-168.5	−1.3
3 Nov. 1979, N	6	144-161	149.8	38.2	143.6-150.0	126.9-172.7	−1.9
15 Nov. 1979, D	5	144-164	152.4	56.3	143.8-161.0	122.1-182.7	+2.6
1 Dec. 1979, N	12	144-153	148.7	7.9	146.9-150.5	140.1-157.3	−3.7
14 Dec. 1979, D	4	150-164	157.6	19.7	151.3-163.7	137.1-177.9	+8.8
3 Jan. 1980, N	8	154-170	161.5	20.3	156.8-165.2	146.4-176.6	−4.0
16 Jan. 1980, D	1	164	164.0	0	164.0	164.0	+2.5
4 Feb. 1980, N	2	155-157	156.5	0.5	154.3-158.7	149.5-163.5	−7.5
15 Feb. 1980, D	4	156-165	162.2	17.6	155.4-168.0	142.9-181.5	+5.7
5 Mar. 1980, N	4	154-175	164.5	77.7	152.3-176.7	116.1-205.1	+2.3
19 Mar. 1980, D	3	155-158	156.7	1.3	154.6-158.8	150.0-163.4	−7.8
			1978 Year Class				
14 Apr. 1978, D	7	29- 40	32.3	11.9	29.2- 35.4	20.2- 44.4	
8 May 1978, D	0	—	—	—	—	—	
14 June 1978, D	305	50- 76	64.9	19.5	64.4- 65.4	53.5- 76.3	+32.6*
15 July 1978, D	781	51- 93	79.0	17.6	78.7- 79.3	68.2- 89.8	+14.1*
15 Sept. 1978, D	134	78-111	98.7	25.4	97.8- 99.6	85.7-111.7	+19.7*
11 Oct. 1978, N	238	93-131	109.2	35.8	108.4-110.0	93.8-124.6	+10.5*
1 Dec. 1978, N	664	98-135	114.3	28.2	113.9-114.7	100.6-128.0	+5.1*
13 Dec. 1978, D	888	100-135	117.8	26.9	117.5-118.1	104.4-131.2	+3.5*
24 Feb. 1979, D	112	107-133	121.8	40.9	120.6-123.0	105.3-138.3	+4.0*
12 Mar. 1979, N	1,501	96-145	120.7	65.1	120.3-121.1	99.9-141.5	−1.1*
5 Apr. 1979, N	1,132	98-150	121.4	64.9	120.9-121.9	100.6-142.2	+7.0*
20 Apr. 1979, D	241	110-146	123.5	39.7	122.7-124.3	107.3-139.7	+2.1*
14 May 1979, N	389	100-138	119.8	33.7	118.9-120.7	104.8-134.8	−3.7*
6 June 1979, N	988	100-144	119.5	48.9	119.4-119.6	101.5-137.5	−0.3*
21 June 1979, D	135	100-143	121.7	47.3	120.5-122.9	104.0-139.4	+2.2*
5 July 1979, N	73	101-145	121.4	59.2	120.9-121.9	101.6-141.2	−0.3*
19 July 1979, D	46	110-144	122.2	34.2	120.5-123.9	106.4-138.0	+0.8*
22 Aug. 1979, D	202	105-145	124.4	42.3	123.5-125.3	107.6-141.2	+2.2*
22 Sept. 1979, D	190	110-145	125.6	30.4	124.8-126.4	111.4-139.8	+1.2*
2 Oct. 1979, N	209	110-144	124.7	50.5	123.7-125.7	106.4-143.0	−0.9*
16 Oct. 1979, D	212	113-144	127.6	38.7	126.8-128.4	111.6-143.6	+3.6*
3 Nov. 1979, N	410	116-143	127.3	35.9	126.7-127.9	111.9-142.7	−0.3*
15 Nov. 1979, D	88	116-143	128.6	37.9	127.3-129.9	112.7-144.5	+1.3*
1 Dec. 1979, N	608	116-143	129.0	45.1	128.5-129.5	111.7-146.3	+0.4*
14 Dec. 1979, D	175	116-149	131.9	71.9	130.6-133.2	110.1-153.7	+2.9*
3 Jan. 1980, N	647	116-153	131.6	48.3	131.1-132.1	113.7-149.5	−0.3*
16 Jan. 1980, D	418	116-155	131.4	54.8	130.7-132.1	112.3-150.5	−0.2*
4 Feb. 1980, N	769	116-154	131.3	54.0	130.8-131.6	112.4-150.2	−0.1*
15 Feb. 1980, D	153	120-155	132.2	44.1	131.2-133.4	115.2-149.4	+1.0*
5 Mar. 1980, N	464	120-153	133.9	44.0	133.3-134.5	116.8-151.0	+1.6*
19 Mar. 1980, D	234	120-154	133.7	53.6	132.8-134.6	114.8-152.6	−0.2*

TABLE 2.—*Continued.*

Collection date	*n*	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1979 Year Class				
14 May 1979, N	89	22- 49	27 6	10 5	26 9- 28.3	19 3- 35.9	
6 June 1979, N	207	29- 69	43 7	59 0	42.7- 44 7	23.9- 63.5	+16 1*
21 June 1979, D	111	35- 74	50 8	44 3	50 2- 51 4	33 7- 67.9	+7 1*
5 July 1979, N	220	30- 76	55.0	74 1	73 0- 75 2	32 8- 77 2	+4 2*
19 July 1979, D	17	40- 80	69 2	76 9	64 7- 73 7	46 6- 91 8	+14 2*
22 Aug 1979, D	9	63- 81	72.9	33.1	68 8- 77 2	58 1- 87 7	+3 7*
22 Sept. 1979, D	247	58-102	83.3	78.8	77 7- 79.9	60.4-106 2	+10 4*
2 Oct. 1979, N	4,933	58-109	83 7	24 3	83.6- 83.8	71 0- 96 4	+0 4*
16 Oct. 1979, D	363	70-112	89 4	50 9	88.7- 90.1	71.0-107 8	+5 7*
3 Nov. 1979, N	355	72-115	96.8	36.5	96.2- 97 4	81.2-112 4	+7 4*
15 Nov. 1979, D	155	87-115	100.4	18.0	99 7-101.1	89 5-111 3	+3 6*
1 Dec. 1979, N	525	88-115	100.5	21.3	100.1-100.9	88 6-112 4	+0 1*
14 Dec. 1979, D	136	91-115	102.6	15 9	101.9-103.3	92.3-112.9	+2 1*
3 Jan. 1980, N	198	91-115	104 6	17 8	104.0-105 2	93.7-115.5	+2.0*
16 Jan. 1980, D	138	94-115	104 1	16.4	103.4-104 8	93 7-114.5	+0 5*
4 Feb. 1980, N	223	91-115	105 7	23.3	105 1-106.3	93.3-118 1	+1 6*
15 Feb. 1980, D	223	96-119	107.3	25.3	106.6-108 0	94.3-120 3	+1 6*
5 Mar. 1980, N	243	98-119	109 4	17.7	108.9-110 0	98.6-120 2	+2 1*
19 Mar. 1980, D	225	96-119	107.7	27 4	107.0-108.4	94 2-121.2	−1 7*

proposed a spring or late winter-early spring spawning period (Hildebrand 1954; Miller 1965; Chittenden and McEachran 1976) based on the captures of fish 106-159 mm TL with well-developed gonads in February (Hildebrand 1954) and fish 31-89 mm TL in early May and June (Caldwell 1955; Miller 1965). Henwood's (1975) histological studies indicated spawning from November through April, but our data indicate little or no spawning before January. Our finding that

TABLE 3.—Analyses of the monthly regressions of ovary weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, December 1978-March 1980. Regressions were significant (at $\alpha = 0.05$) except on 11 October 1978, 6 June 1979, 19 July 1979, 22 August 1979, and 22 September 1979.

Cruise	*n*	100 r^2	Equation
1 Dec. 1978	144	23 70	$Y = -0.963 + 0.010\,X$
24 Feb. 1979	41	17 89	$Y = 0.913 + 0.016\,X$
12 Mar. 1979	168	37.35	$Y = -3.096 + 0.038\,X$
5 Apr. 1979	109	48.18	$Y = -3.295 + 0.036\,X$
20 Apr. 1979	84	7.00	$Y = -0.496 + 0.008\,X$
14 May 1979	110	23 26	$Y = -0.166 + 0.002\,X$
5 July 1979	24	36.97	$Y = -0.333 + 0.004\,X$
2 Oct. 1979	79	41.52	$Y = -0.352 + 0.004\,X$
16 Oct. 1979	53	10.58	$Y = -0.109 + 0.002\,X$
3 Nov. 1979	89	47.78	$Y = -0.232 + 0.003\,X$
15 Nov. 1979	65	58 86	$Y = -0.564 + 0.007\,X$
1 Dec. 1979	68	71.36	$Y = -1.486 + 0.016\,X$
14 Dec. 1979	83	62 26	$Y = -1.450 + 0.016\,X$
3 Jan. 1980	97	51.04	$Y = -1.613 + 0.020\,X$
16 Jan. 1980	85	82 36	$Y = -2.329 + 0.026\,X$
4 Feb. 1980	93	73 57	$Y = -3.132 + 0.036\,X$
15 Feb. 1980	79	59 02	$Y = -1.962 + 0.024\,X$
5 Mar. 1980	81	48 07	$Y = -2.203 + 0.028\,X$
19 Mar. 1980	64	69.22	$Y = -2.148 + 0.026\,X$

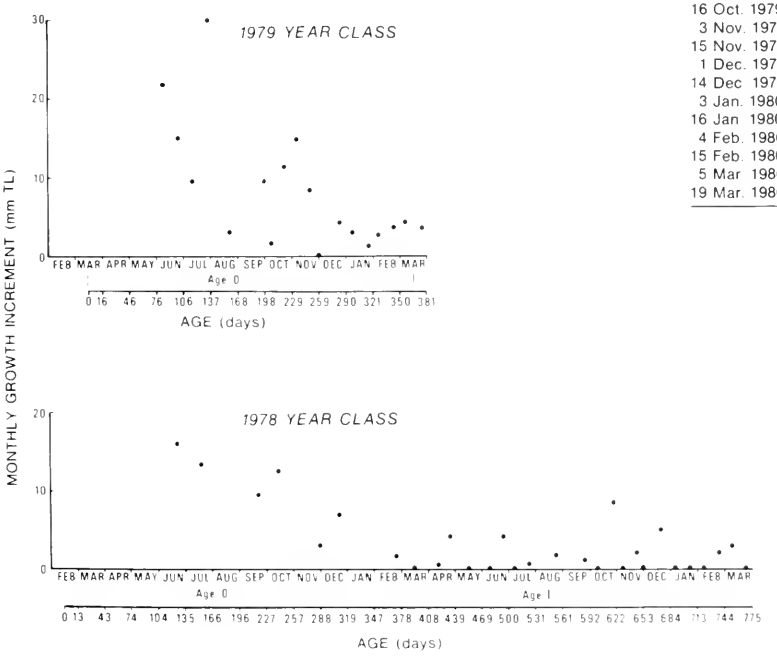


FIGURE 3.—Monthly growth increments for the 1978 and 1979 year classes of *Stenotomus caprinus*. Unadjusted growth increments (Table 2) were converted to growth per 30 d. Negative growth was rounded to 0.

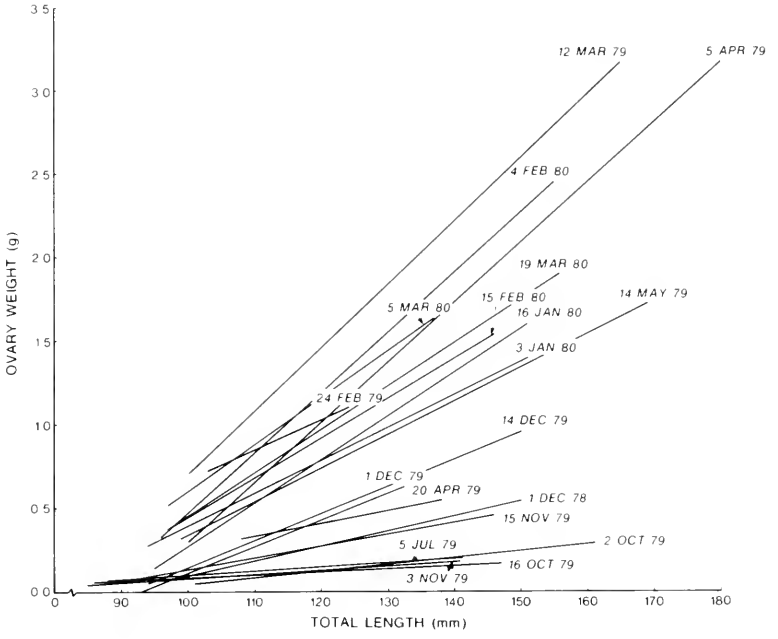


FIGURE 4.—Monthly ovary weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

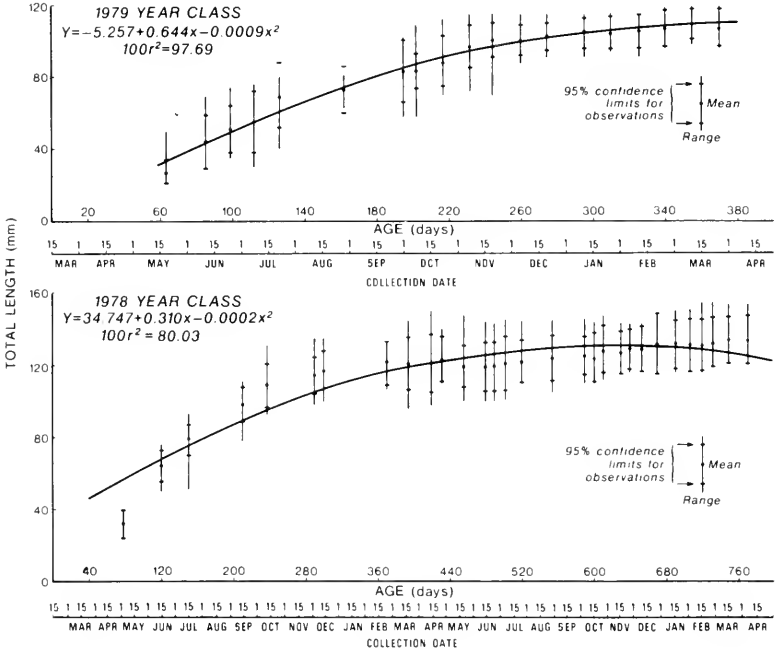


FIGURE 5.—Mean observed and predicted sizes at age for the 1978 and 1979 year classes of *Stenotomus caprinus*. Mean sizes at age (Table 2) were regressed on age after assigned hatching dates of 15 February and 15 March for these respective year classes. Regressions were significant at $\alpha = 0.05$.

virtually all *S. caprinus* spawn at 12 mo of age has not been reported, nor has the discrete and short duration of spawning been recognized. Sex ratios have not been reported for *S. caprinus*, although 1:1 and 1:1.26 male to female ratios have been reported for its congener *S. chrysops* (Smith and Norcross 1968; Morse 1978). The pattern of spawning in *S. caprinus* is several months earlier in timing but similar to *S. chrysops* which spawns once a year from May through August

with greatest spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a).

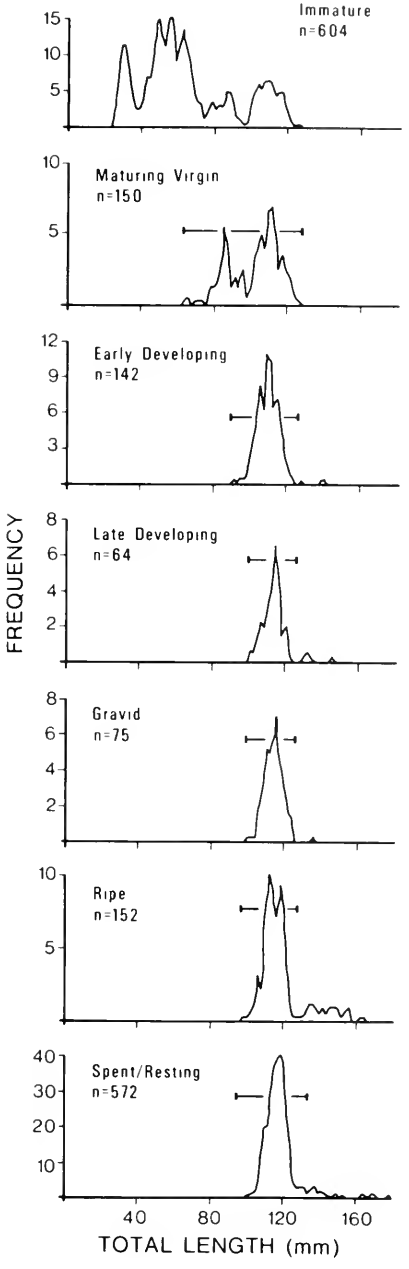


FIGURE 6.—Length frequencies (moving averages of three) of immature and female *Stenotomus caprinus* by maturity stages. See Table 1 for definitions of maturity stages. Brackets indicate size ranges used to calculate the mean length of fish approaching age I for each maturity stage.

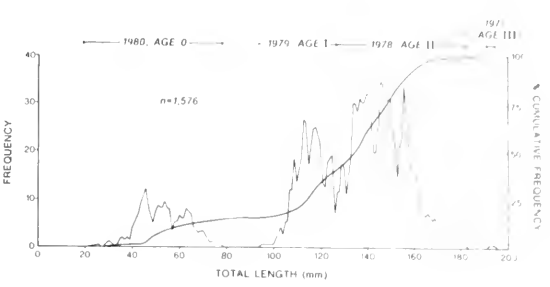


FIGURE 7.—Length frequency (moving averages of three) of *Stenotomus caprinus* captured in the north central Gulf aboard the *Oregon II*, 10 April-1 May 1980. Probable ages and year class identities are indicated.

MOVEMENTS, SPAWNING AREAS, AND DIEL VARIATION IN CATCH

Results

Stenotomus caprinus exhibit size and age gradients with depth related to their movements, spawning areas, and recruitment. Although captured from 18 m to 100 m (Fig. 9), they were most common between 36 m and 55 m.

Young-of-the-year recruited in inshore waters during the spring and moved towards deeper water as they grew. Recently hatched fish 20-50 mm TL appeared only in 18-27 m depths in the period February-May (Fig. 9), but became distributed as deep as 36-47 m by June to September. The larger young-of-the-year continued to disperse gradually to deeper water as indicated by their size gradients with depth in June-September 1979 and in October 1979-January 1980.

Adult *S. caprinus* reside and spawn in waters deeper than 27 m. No adults were found in waters shallower than 27 m during the January-April spawning period (Fig. 9). Fish of ages I and II occurred in waters deeper than 27 m throughout the year but showed no size gradient with depth. This indicates that they were uniformly mixed throughout the 27-100 m depth range.

Stenotomus caprinus appear most vulnerable to trawling at night. Mean catch per tow at night in the 18-100 m depth range that *S. caprinus* occupies averaged three times that of day catches on 10 of 11 occasions in the period December 1978-March 1980 when day and night cruises were made each month or close together in time (Fig. 2).

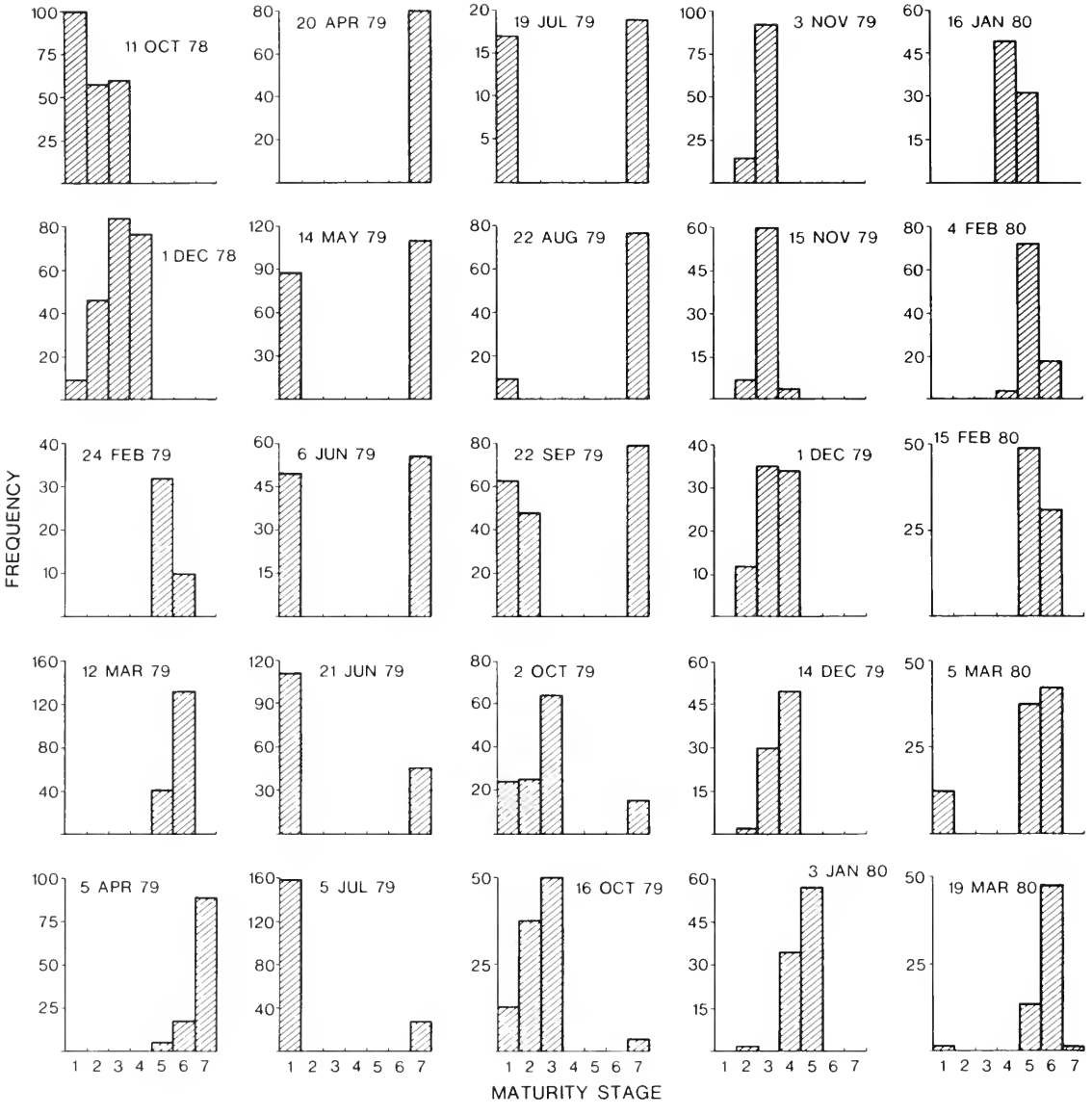


FIGURE 8.—Monthly maturity stages of female *Stenotomus caprinus*. Maturity stages are described in Table 1.

Discussion

The spawning periodicity of *S. caprinus* appears timed to coincide with the late winter-early spring periodicity of onshore surface currents on the continental shelf of the northwestern Gulf. Rising sea levels in the period January-April (Marmer 1954) coincide with onshore surface currents (Kimsey and Temple 1963; Smith 1975). This current system could transport eggs and larvae from offshore spawning areas to inshore nurseries where the young recruit, assuming that *S. caprinus* have pelagic eggs and larvae like *S. chrysops* (Johnson 1978).

Our findings on the movements and distribution of *S. caprinus* agree with the literature. The size-depth relationship in which younger individuals occur inshore in the spring has been reported (Hildebrand 1954; Caldwell 1955; Miller 1965). Our findings on size-depth gradients during the summer support Henwood's (1975) suggestion that young-of-the-year gradually dis-

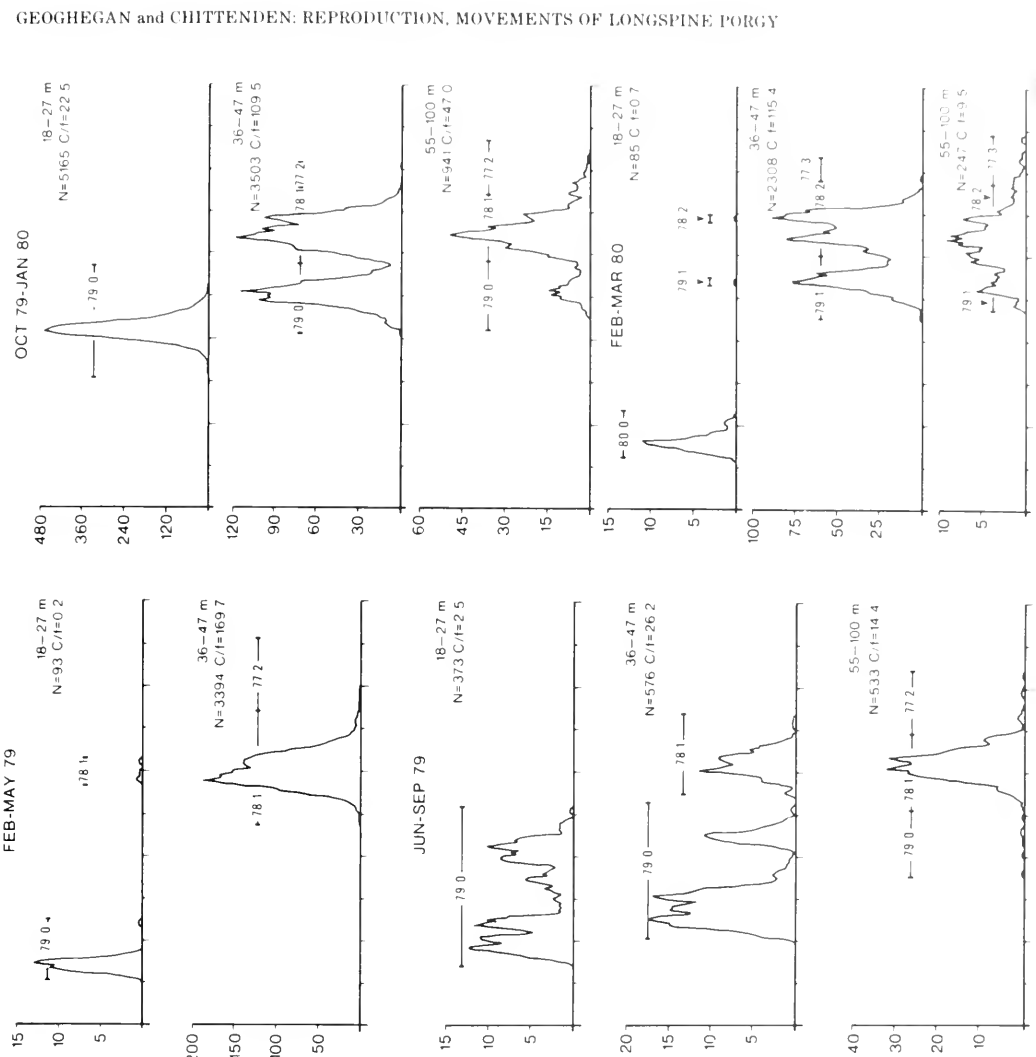


FIGURE 9.—Length frequencies (moving averages of three) by depth for *Stenotomus caprinus* off Freeport, Tex. Multiple peaks within size ranges designated as age 0 reflect growth. C/f indicates number of individuals per 10-min tow.

perse to deeper water. Our finding that age-I and age-II fish show no size-depth gradient and are mixed throughout 27-100 m depths has not been reported but agrees with Moore's (1964) finding that average weight did not increase in waters deeper than 64 m.

Our findings that *S. caprinus* is most vulnerable to trawling at night has not been reported, although similar behavior has been recorded for *S. aculeatus* (Powles and Barans 1980). Fritz (1965) found that *S. chrysops* made up a greater percentage of the catch at night, although Smith and Norcross (1968) reported crepuscular catches were greatest. Henwood et al. (1978) suggested that *S. caprinus* actively feeds during the day. These fish might be inactive and near the bottom at night, and thus more vulnerable to trawling.

AGE DETERMINATION USING SCALES

Results

Stenotomus caprinus cannot be aged readily using scales. Scales from 2,342 fish were examined for annuli using criteria of Dery and Rearden (footnote 7) which include cutting over, irregular spacing, and breaking of circuli. Marks similar to annuli were occasionally observed, but these marks varied greatly between scales from the same fish and between fish of the same size, age by length-frequency analysis, and date of capture. Annuli frequently were not apparent on fish that must have been age II or III according to length-frequency analysis, although one important criterion for valid use of the scale method (Lagler 1956; Tesch 1971) is that this procedure should agree with ages determined from length frequencies.

Discussion

Our finding that it is difficult to age *S. caprinus* using scales agrees with Henwood (1975). In contrast, several authors have used scales successfully to age *S. chrysops* (Finkelstein 1969a; Hamer 1979[9]); although this becomes difficult beyond age III (Smith and Norcross 1968).

Stenotomus caprinus are best aged using length frequencies, particularly if, as in the present study, there is a long-term set of data from cruises made close together in time. Under these conditions age determination by length-frequency analysis may be obvious, as we found. Length-frequency analysis would be less reliable if cruises were several months apart in time, because year class frequencies could merge after age I as our data indicate. The superior merits of age determination by length-frequency analysis are not surprising for *S. caprinus* because 1) this species spawns once a year in a discrete period, 2) within year class frequencies appear normally distributed, and 3) growth of large and small fish within a year class is uniform as evidenced by the observed constant variance. In addition, length-frequency analysis generally is most clear for younger ages (Lagler 1956; Tesch 1971), and *S. caprinus* only lives a few years (see section on Mortality and Postspawning Survival).

AGE DETERMINATION AND GROWTH USING LENGTH-FREQUENCY ANALYSIS

Results

No more than four year classes of *S. caprinus* were present at any time off Texas and only one or two predominated. These year classes represented young-of-the-year and ages I, II, and III (Fig. 2). Only one year class predominated in any month from October 1977 through April 1979, although two year classes often were captured. The 1977 year class predominated initially in this period but virtually disappeared at age I after the 1978 year class recruited. Three year classes usually were captured after the 1979 year class recruited in May. In contrast to the virtual disappearance of the 1977 year class, the 1978 year class remained abundant at age I after the new year class recruited. As a result, two year classes (1978 and 1979) were equally predominant from May 1979 through March 1980. Four year classes were present after the 1980 year class recruited in February, but only the 1978 and 1979 year classes predominated.

Minor qualifications should be noted to the designation of the 1977 year class. The group identified as the 1977 year class in the period December 1977-April 1978 may contain members of the 1976 year class. This is suggested because 1) the size range of fish in that period may be too broad for one year class; 2) apparent

[9]Hamer, P. 1979. Studies of the scup, *Stenotomus chrysops*, in the Mid-Atlantic Bight. N.J. Div. Fish, Game, Shellfish., Necote Creek Res. Stn., Misc. Rep. 18m, 66 p.

growth between October and December 1977 is high when compared with the same period in other years; and 3) size at age I is comparatively large for the 1977 year class. The 1977 and 1978 year classes were difficult to distinguish after December 1978, so that the 1977 year class thereafter may include fast growing members of the 1978 year class.

Stenotomus caprinus growth varied between year classes, but sizes averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Observed mean sizes at age I, based on pooled data from February and March (Table 2), were 134.2 mm TL for the 1977 year class (range 113-157 mm), 120.8 mm for the 1978 year class (range 96-145 mm), and 107.5 mm for the 1979 year class (range 91-119 mm). These sizes at age I agree with regression predictions (Fig. 5) of 114.8 mm TL for the 1978 year class and 110.0 mm for the 1979 year class. Observed mean size at age II was 132.5 mm TL for the 1978 year class (range 116-155) (Table 2), which closely agrees with a regression prediction of 128.6 mm (Fig. 5). The few survivors of the 1977 year class averaged 155.8 mm TL (range 146-182) at age II and 160.8 mm at age III (range 154-175 mm) (Table 2). Many fish approached the maxima in the size ranges at age cited for each year class, and the ranges at age appeared constant between collections indicating uniform growth (Table 2).

Possible error in assigned hatching dates would have little effect on our estimates for mean sizes at age because 99% confidence intervals of observations were constant within the following periods (Table 2): December 1977-April 1978 for the 1977 year class; December 1978-June 1979 for the 1978 year class; and December 1979-March 1980 for the 1979 year class.

Stenotomus caprinus grow rapidly in their first 8 mo, but growth slows greatly as they mature and appears negligible after maturity. The 1978 and 1979 year classes showed a rapid, almost linear decline in monthly growth increments during their first 8 mo (Fig. 3). Growth of the 1978 year class averaged 13.62 mm TL/30 d from 15 February through early October 1978, and the 1979 year class averaged 12.66 mm/30 d from 15 March to early November 1979, ignoring the regression effect. In contrast, the 1978 year class grew only 13 mm TL in its second year; and the 1977 year class grew only 23 mm in its second year and 4 mm in its third year. This growth pattern may result in gradual merging of year class size compositions after age I as indicated by the 1978 and 1979 year classes (Fig. 2). The small amount of growth after maturity seems to occur primarily during the late spring-early fall interim between reproductive activities (Fig. 3). Very little growth occurred in the January-April spawning period when the 1978 year class averaged 0.83 mm TL/30 d in that period in 1979 and 0.80 mm/30 d in 1980.

Size at age I varies between *S. caprinus* year classes, but growth is not obviously density dependent. No simple relationship was apparent for the 1977-79 year classes (Fig. 10) between mean size at age I and their index of year class strength, calculated as $\Sigma c_i/\Sigma f_i$ where Σf_i is the total number of tows and Σc_i is the total catch at age I for each year class at depths of 27-47 m. Fish of the weak 1979 year class averaged smaller at age I (107.5 mm TL) than the strong 1978 year class (120.8 mm), a pattern not consistent with density dependent growth. Growth of the 1979 year class might have been depressed by interaction with the strong 1978 year class, but no density dependent relationship was apparent even when a pooled index of population strength was substituted for the 1979 year class strength index.

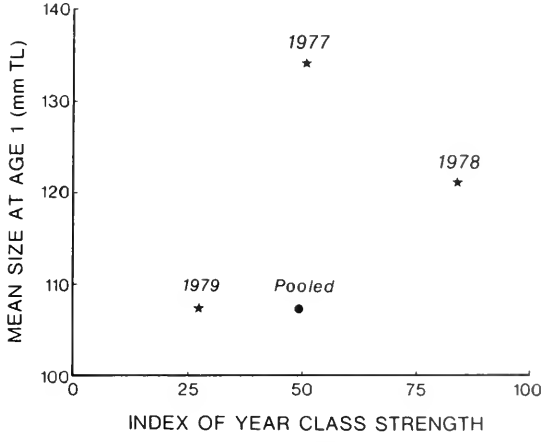


FIGURE 10.—Relationship between mean sizes at age I and year class strength for *Stenotomus caprinus* off Freeport, Tex. Indices of individual year class strength are indicated by stars and the pooled index by solid circle.

Discussion

Our findings on growth are largely new because the growth of *S. caprinus* has not been described previously. Sizes at age I agree with Chittenden and McEachran's (1976) suggestion

that *S. caprinus* reaches 90-123 mm TL at age I. Back-calculated lengths of *S. chrysops* are 120-155 mm TL at age I and 182-213 mm at age II (Finkelstein 1969a; Hamer footnote 9). Sizes at age I appear to be similar in these species, but *S. chrysops* is much larger at age II. Our growth data and the constant size noted in later gonad maturity stages (Fig. 6) indicate that *S. caprinus* markedly diverts energy from somatic growth to gonadal development as it matures. The different sizes of these congeners at age II probably reflect this drastic diversion of energy in *S. caprinus*.

MAXIMUM SIZE AND LIFESPAN

Results

The maximum size typically reached by *S. caprinus* is about 200 mm TL. The largest fish collected off Texas ($n = 22,924$) was 182 mm TL, and the largest specimen collected in the north central Gulf ($n = 1,576$) aboard the *Oregon II* was 193 mm TL.

The maximum lifespan of *S. caprinus* typically appears to be 2.5-3 yr. In the period October 1977-March 1980, 99% of the specimens captured off Texas were <146 mm TL, and 99.5% were <149 mm (Fig. 11). Many age II fish captured off Texas were as large as 155 mm TL. The largest fish collected was age II when captured in March 1979, or age III if it was a member of the poorly defined 1976 year class (Fig. 2). These data indicate that a value of $t_L = 2.5$-3 yr is reasonable for this Beverton-Holt model parameter (Gulland 1969). This estimate is supported by data from the north central Gulf (Fig. 7) in which 99% of the fish were <172 mm TL and 99.5% were <176 mm. Fish of these sizes were age II or III in the north central Gulf (Fig. 7).

Discussion

The maximum sizes reported herein are slightly larger than the maximum size reported by Hildebrand (1954), Caldwell (1955), and Chittenden and McEachran (1976). The only published record of *S. caprinus* much larger than 200 mm TL is that of Franks et al. (1972) who captured a specimen 256 mm TL in the north central Gulf. The apparent larger size of individuals at given percentages of the catch in the north central Gulf might reflect growth differences between areas, or the nonrandom sub-

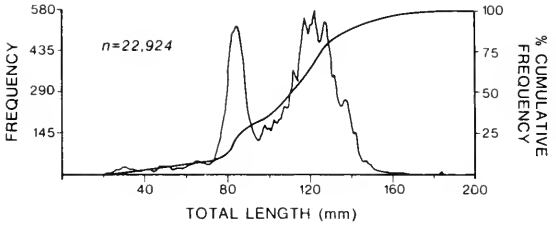


FIGURE 11.—Length frequency (moving averages of three) and cumulative percent frequency of all *Stenotomus caprinus* collected off Freeport, Tex., October 1977-March 1980.

sampling from the *Oregon II* catch which would probably select larger fish. Values of t_L would vary from year to year due to variation in postspawning survival noted later.

MORTALITY AND POSTSPAWNING SURVIVAL

Results

Stenotomus caprinus has a total annual mortality rate of about 83-99% on a time-specific basis. Time-specific total annual mortality rates ($1 - S$) were calculated from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish collected at age each cruise in depths of 18-100 m. The pooled estimate, using Heincke's procedure (Ricker 1975) was 98.95% comparing the 1977 and 1978 year classes and individual rates generally exceeded 98%. These values probably overestimate $1 - S$, because the 1978 year class was stronger than the 1977 year class (Fig. 10). The pooled estimate comparing the apparent 1976 and 1977 year classes was 99.79%. The pooled estimate comparing the 1978 and 1979 year classes was 84.94% which may be fortuitous because it included one data set (October 1979) for which an exceptionally large number of fish from the 1979 year class were captured. A minimum pooled mortality estimate for the 1978 and 1979 year classes is 40.73%, if the exceptional October 1979 data set is excluded. This is probably a large underestimate because the 1979 year class was so much weaker than the 1978 year class. Realistic estimates could not be calculated in most instances comparing the 1978 and 1979 year classes because N_t exceeded N_0, which largely reflects the much greater strength of the 1978 year class (Fig. 10). Time-specific mortality estimates made from Chittenden and McEachran's (1976)

raw data were 99% for late September 1973 ($S = 5/435$) and 83% for January 1974 ($S = 395/2,468$). Pooled cohort-specific estimates of $1 - S$ were 99.23% for the 1977 year class and 83.36% for the 1978 year class using Heincke's procedure. The different mortality rates for these year classes are consistent with theoretical mortality rates given later, and the greater postspawning survival of the 1978 year class.

Postspawning survival of *S. caprinus*, total annual mortality rates, and maximum lifespan varies greatly between years and year classes. The 1977 and apparently 1976 year classes rarely appeared after they spawned at age I (Fig. 2). In contrast, many members of the 1978 year class survived after spawning at age I and spawned again at age II. White and Chittenden (1977) suggested somatic weight variation as a factor in the survival of the Atlantic croaker, *Micropogonias undulatus*. Somatic weight of female *S. caprinus* did not change in a regular monthly pattern, and regression elevations differed widely in consecutive months (Fig. 12, Table 4).

TABLE 4.—Analyses for the monthly regressions of somatic weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, October 1978-March 1980. All regressions were significant at $\alpha = 0.05$.

Collection date	n	100 r^2	Equation
11 Oct. 1978	53	86.01	$Y = -50.789 + 0.699\ X$
1 Dec. 1978	144	87.44	$Y = 71.240 - 1.323\ X + 0.008\ X^2$
24 Feb. 1979	41	78.88	$Y = -32.009 + 0.506\ X$
12 Mar. 1979	168	94.57	$Y = 73.409 - 1.361\ X + 0.008\ X^2$
5 Apr. 1979	109	97.15	$Y = 59.722 - 1.234\ X + 0.008\ X^2$
20 Apr. 1979	84	80.36	$Y = 234.333 - 4.095\ X \quad 0.020\ X^2$
14 May 1979	110	84.32	$Y = 68.022 - 1.327\ X + 0.008\ X^2$
6 June 1979	56	92.71	$Y = -69.449 + 0.843\ X$
21 June 1979	49	70.44	$Y = -34.932 + 0.539\ X$
5 July 1979	24	91.41	$Y = 137.564 - 2.44\ X + 0.013\ X^2$
19 July 1979	20	60.11	$Y = -48.541 + 0.663\ X$
22 Aug. 1979	70	80.01	$Y = 186.455 \quad 3.150\ X + 0.015\ X^2$
22 Sept. 1979	82	68.32	$Y = -38.548 + 0.584\ X$
2 Oct. 1979	79	95.62	$Y = 71.630 + 1.233\ X + 0.007\ X^2$
16 Oct. 1979	53	88.69	$Y = -44.643 + 0.631\ X$
3 Nov. 1979	89	93.90	$Y = -37.481 + 0.578\ X$
15 Nov. 1979	65	95.70	$Y = 4.819 - 0.237\ X + 0.004\ X^2$
1 Dec. 1979	37	68.44	$Y = -30.428 + 0.508\ X$
14 Dec. 1979	82	96.32	$Y = -43.178 + 0.609\ X$
3 Jan. 1980	96	95.34	$Y = 35.286 \quad 0.762\ X + 0.006\ X^2$
16 Jan. 1980	86	97.36	$Y = 35.576 - 0.795\ X + 0.006\ X^2$
4 Feb. 1980	93	97.57	$Y = 20.722 - 0.526\ X + 0.005\ X^2$
15 Feb. 1980	79	96.23	$Y = 20.382 - 0.506\ X + 0.005\ X^2$
5 Mar. 1980	80	83.65	$Y = -38.256 + 0.565\ X$
19 Mar. 1980	64	79.38	$Y = -49.710 + 0.662\ X$

Discussion

Both time-specific and cohort-specific estimates indicate that the total annual mortality rate of *S. caprinus* is about 83-99%, depending on postspawning survival. Lower values in this range agree with theory (Royce 1972:238) that total annual mortality is 78-84% if the maximum age is 2.5-3 yr as observed. Higher values are consistent with theoretical annual rates of 90-100% given the 1-2 yr lifespan observed for some year classes.

Variation in postspawning survival might not be due to somatic weight changes because of the lack of a regular monthly pattern and the wide variation in regression elevations between adjacent months, although our somatic weight regressions are based primarily on the 1978 and 1979 year classes which did not disappear after spawning.

TOTAL WEIGHT-TOTAL LENGTH, GIRTH-TOTAL LENGTH, AND LENGTH-LENGTH RELATIONSHIPS

Regression and related analyses for total weight-total length, girth-total length, and length-length relationships are presented in Table 5.

Total length-total weight regressions for adult males and females were not significantly different in slope ($F = 0.029$, df = 1,657, $\alpha = 0.05$) or in adjusted means ($F = 1.63$, df = 1,658, $\alpha = 0.05$) so that one pooled regression equation was presented for them. Calculated slopes varied significantly from $\beta = 3.0$ ($t = 13.2$, df = 1,682, $\alpha = 0.05$) except when data for immatures, males, and females were pooled ($t = 0.197$, df = 2,792, $\alpha = 0.05$).

GENERAL DISCUSSION

Stenotomus caprinus, which inhabits the warm temperate Gulf, exhibits markedly different population dynamics from *Stenotomus chrysops*, which primarily inhabits the cold temperate Atlantic north of Cape Hatteras, N.C. Our data and the literature agree that for *S. caprinus*: 1) spawning occurs in one discrete period a year with peak spawning in February or March; 2) all individuals reach maturity and spawn at 90-125 mm TL as they approach age I; 3) maximum size typically is about 200 mm TL, but most fish are much smaller; 4) maximum lifespan is 2.5-3 yr; 5) total annual mortality rate is 83-99%, but postspawning survival, total annual mortality rates, and lifespan vary between year classes; and 6) average sizes are 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. In contrast, *S. chrysops* north of Cape Hatteras 1)

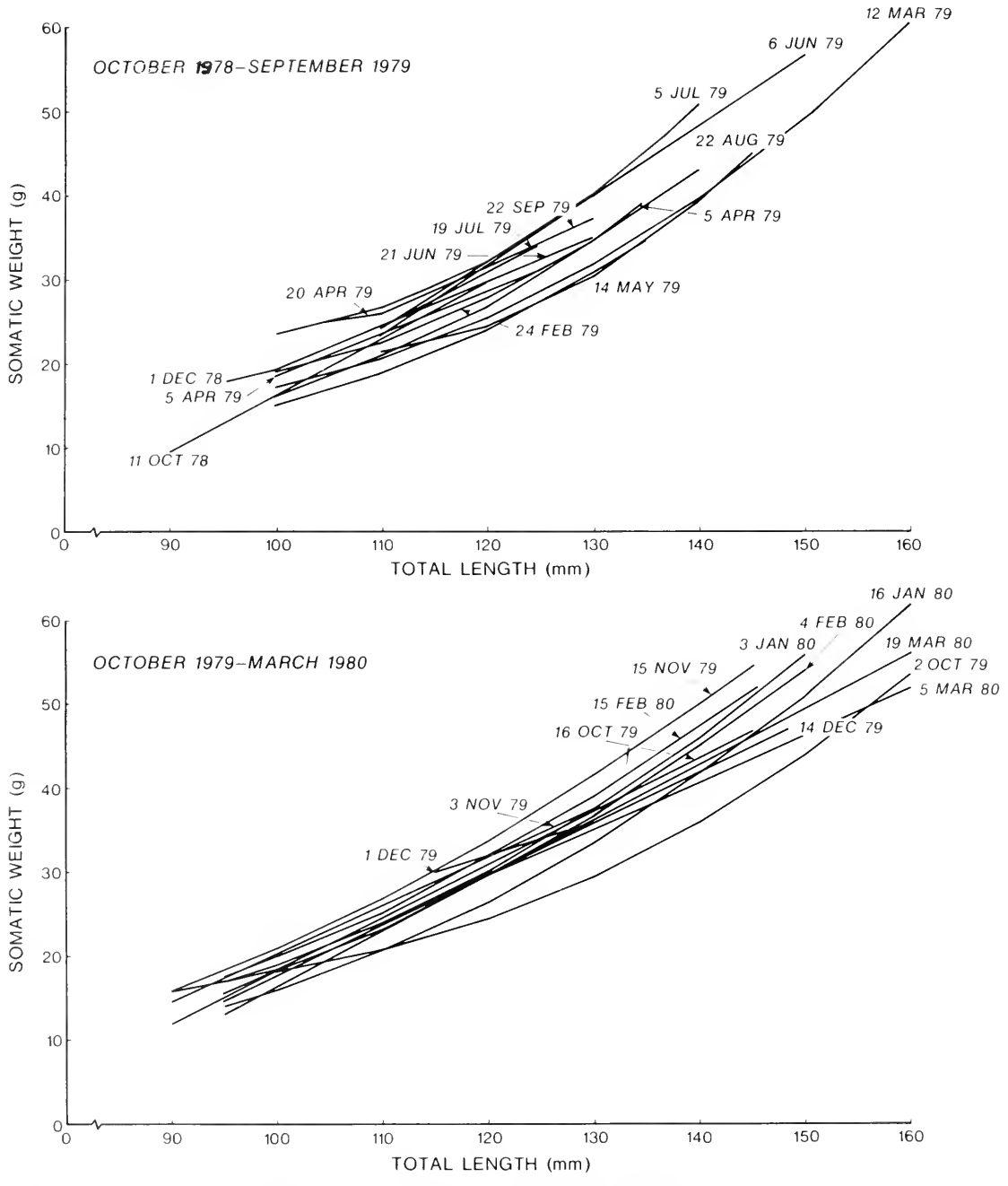


FIGURE 12.—Monthly somatic weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

spawns in the period May-August with peak spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a); 2) reaches maturity at age II at 182-213 mm TL (Finkelstein 1969a, b; Hamer footnote 9); 3) reaches a maximum size of approximately 480 mm TL (Hamer footnote 9); 4) has a maximum lifespan of 15 yr (Finkelstein 1969a); 5) apparently has a much lower total an-

TABLE 5.—Analyses of total length-total weight (A), length-length (B), and total length-girth (B) relationships for *Stenotomus caprinus*. Lengths and girths are in millimeters and weights are in grams. All regressions were significant at $\alpha = 0.05$. See Methods and Materials for symbols.

Relation	Equation	n	100 r^2	Residual mean square	Corrected total SS for both variables	Means of variables	Observed TL range (not transformed)
A. All fish	$\text{Log}_{10}TW = -4.85 + 3.05\ \text{Log}_{10}TL$	2,793	99.32	0.0017	Log TW = 705.12 Log TL = 75.17	Log TW = 1.28 Log TL = 2.01	21-182
Adult fish	$\text{Log}_{10}TW = -4.13 + 2.71\ \text{Log}_{10}TL$	1,683	90.51	0.0010	Log TW = 18.27 Log TL = 2.25	Log TW = 1.50 Log TL = 2.08	91-182

Relation	Equation	n	100 r^2	Residual mean square	Corrected total SS for dependent variable	Mean of dependent variable	Observed range for dependent variable (not transformed)
B. SL-TL	SL = 0.41 + 0.76 TL	2,776	99.26	3.55	1,326,361.42	81.88	21-182
TL-SL	TL = 0.26 + 1.31 SL	2,776	99.26	6.10	2,280,443.91	116.86	21-182
SL-FL	SL = 0.85 + 0.11 FL	2,421	97.12	4.01	337,068.73	81.88	26-182
FL-SL	FL = 2.90 + 1.14 SL	2,421	97.12	5.40	453,813.15	104.88	26-182
FL-TL	FL = 1.99 + 0.88 TL	2,402	97.36	4.98	452,549.20	104.88	26-182
TL-FL	TL = 0.93 + 1.11 FL	2,402	97.36	6.24	567,821.45	116.86	26-182
TL-G	TL = 8.27 + 0.94 G	2,792	98.00	16.32	2,286,249.29	107.26	21-182
G-TL	G = −6.54 + 1.04 TL	2,792	98.00	18.17	2,545,019.98	105.50	21-182

nual mortality rate, theoretically 26% based on a 15-yr lifespan (Royce 1972:238); and 6) averages 120-155 mm TL at age I, 183-213 mm at age II, and 232-257 mm at age III (Finkelstein 1969a; Hamer footnote 9).

The basic pattern of population dynamics characteristics enumerated for *S. caprinus* is similar to that reported from the Gulf for *Micropogonias undulatus* (White and Chittenden 1977), *Cynoscion nothus* (DeVries and Chittenden 1982), *C. arenarius* (Shlossman and Chittenden 1981), and *Peprilus burti* (Murphy 1981). These findings give additional support to the suggestions (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics that stresses small size, short lifespan, high mortality rates, and rapid turnover of biomass, especially when compared with congeners or conspecifics north of Cape Hatteras.

The intrageneric variation in *Stenotomus* supports the suggestion of White and Chittenden (1977) that zoogeographic variation in life histories and population dynamics occurs at Cape Hatteras. Unfortunately, the meager information published from the Atlantic coast south of Cape Hatteras does not permit enumeration of population dynamics of *Stenotomus* from that area. However, our findings on *Stenotomus* are consistent with the intrageneric variation in population dynamics within the genus *Cynoscion* at Cape Hatteras (Shlossman and Chittenden 1981), and are similar to the zoogeographic variation reported for *M. undulatus* (White and Chittenden 1977). This zoogeographic variation in population dynamics characteristics has important management implications, because Carolinean Province fish should be less sensitive to growth overfishing than their congeners or conspecifics north of Cape Hatteras.

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VERTICAL MIGRATION AND ITS EFFECT ON DISPERSAL OF PENAEID SHRIMP LARVAE IN THE GULF OF CARPENTARIA, AUSTRALIA

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ABSTRACT

Penaeid shrimp larvae in the Gulf of Carpentaria, Australia, sampled over discrete depths and time intervals showed a day-night pattern of vertical distribution. The magnitude of the migrations increased with larval development. The patterns of vertical distribution were variable and depended strongly on light penetration. Vertical migratory behavior of larvae was linked to currents at various depths. Daily and fortnightly extrapolations of larval displacement showed that vertical migration generally enhanced horizontal advection but the distances and directions were dependent on the current regime and the vertical distribution pattern. It was estimated that larvae could be advected from 70 to 100 km, far enough to traverse the distance from the known spawning grounds to estuarine nursery grounds. Results of this short-term study indicate that differential advection on a seasonal scale may be responsible for the temporal and spatial recruitment patterns of postlarvae observed in the Gulf of Carpentaria.

Vertical migration is widespread among marine and freshwater Crustacea (Russell 1925; Bainbridge 1961). The migration is often periodic and can vary from diurnal and tidal through to seasonal and ontogenetic periodicity. Almost as diverse as the organisms involved are the probable environmental cues that elicit the response and adaptive advantages attributed to this behavior (Bainbridge 1961; Enright 1977; Pearre 1979). Undoubtedly animals have adopted vertical migratory behavior for a variety of immediate and long-term biological advantages (Vinogradov 1968).

Most of the adaptive advantages of vertical migration that have been suggested usually apply to animals that live in relatively deep water with temperature, pressure, light, food, and predator abundance gradients. Shallow-water holoplanktonic and meroplanktonic animals also undergo vertical migrations, however. Because the vertically migrating animal is exposed to different current regimes at different depths (Hardy 1936, 1953), the behavior has been invoked to aid maintenance of position within estuaries (Bousfield 1955; Graham 1972; Weinstein et al. 1980; Wooldridge and Erasmus 1980) and on continental shelves (Walford 1938). It has also been suggested that timed vertical migration enhances horizontal displacement up an estuary (Carriker 1951; Wood and Hargis 1971; Sandifer 1975; Bigford 1979; Sulkin et al. 1980), alongshore (Longhurst 1968; Efford 1970), or onshore (Woodmansee 1966; Penn 1975; Rimmer and Phillips 1979), often against the prevailing currents. In no instance, however, have these mechanisms been demonstrated by monitoring both the vertical behavior and the in situ current regimes simultaneously.

Dispersal, during the pelagic larval phase, is the most likely mechanism that brings postlarval and juvenile penaeid shrimp into shallow-water coastal and estuarine nursery areas from their offshore spawning grounds (Kirkegaard 1975). Evidence of vertical migration of penaeid larvae, which might enhance the onshore movement, is mixed and inconclusive. In the study by Eldred et al. (1965) the larval vertical distribution patterns were variable between species, but appeared to be consistent in the study by Temple and Fischer (1965). A change in behavior from photopositive to photonegative with development was reported by Racek (1959), while a gradual increase in vertical migratory ability, without a phase change, has been seen in other studies (Temple and Fischer 1965; Jones et al. 1970). Most noticeable have been the variable patterns in vertical distribution with varying environmental conditions in studies with repeated sampling (Temple and Fischer 1965; Jones et al. 1970). Nevertheless, based on an idealized larval

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behavior and limited knowledge of current regimes, Penn (1975) hypothesized that larvae of *Penaeus latisulcatus*, off Western Australia, were capable of moving onshore against prevailing currents during certain times of the year.

In this study I attempted to test Penn's (1975) hypothesis by intensively sampling the changes in vertical distribution of penaeid larvae while simultaneously monitoring currents and other environmental parameters in the water column. I hoped to gain insight into the following: the ontogeny of vertical migratory behavior, the environmental factors that control the larval behavior, the current regimes and how they change with depth, and the advective consequences to the larvae resulting from vertical migration through this variable current field.

Staples (1979), studying the postlarvae of *Penaeus merguiensis* in the Gulf of Carpentaria, found discrete temporal and spatial patterns of postlarval recruitment into the rivers around the gulf. These patterns could not be explained entirely by the distribution of adults and the timing of spawning. He proposed that the temporal and spatial patterns of recruitment were caused by the different fates of larvae arising from two peaks of spawning (spring and autumn). While seasonal changes in the direction of larval advection were suggested, little was known about current regimes in the gulf (Cresswell 1971) and nothing known about how these currents would affect the distance and direction of penaeid larval dispersal. This study was, therefore, intended to provide insight into the mechanisms and pathways of larval dispersal and to help explain the variable timing and magnitude of postlarval recruitment.

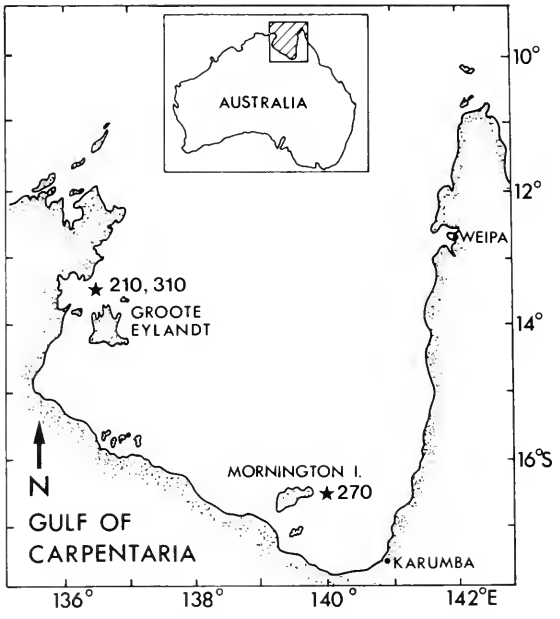

FIGURE 1.—Station numbers and locations for discrete depth sampling (stars) in the Gulf of Carpentaria, Australia.

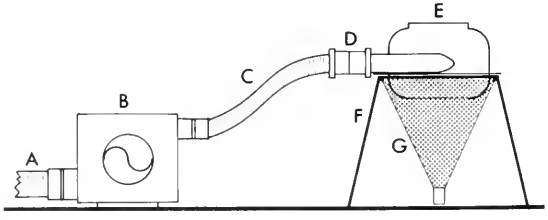

FIGURE 2.—Schematic of pump, water discharge, and filtering system: A) 10.2 cm (4 in) intake hose; B) 7.6 cm (3 in) self-priming centrifugal pump with 6 kW (8 hp) gasoline engine; C) 7.6 cm (3 in) outlet hose; D) quick coupling; E) spinner drum; F) tripod; G) 142 μm mesh plankton net.

MATERIALS AND METHODS

Discrete depth sampling was conducted repeatedly at two locations (Fig. 1) during survey cruises in the Gulf of Carpentaria (Rothlisberg and Jackson 1982). These locations were <30 m in depth and close to known concentrations of adult penaeid shrimp. The ship was anchored on station and a 7.6 cm (3 in) centrifugal pump (Fig. 2), driven by a 6 kW (8 hp) aircooled gasoline engine, was used to pump water from depth. The end of the 10.2 cm (4 in) intake hose was clamped to a weighted wire fed through a meter block. The full length of the hose, in 9.2 m (30 ft) quick coupled lengths, was deployed, regardless of the sampling depth, to prevent variable friction effects. Water from the pump was discharged through a 7.6 cm (3 in) diameter hose tangentially into a drum (spinner) mounted on a tripod. Upon loss of velocity the water drained gently through a 56 cm diameter plankton net (142 μm mesh) suspended beneath the spinner. The outlet hose was coupled to the spinner in such a manner that it could be inserted and withdrawn quickly to allow precisely timed pumping intervals. The pumping rate (up to 1,000 l/min) was monitored with timed fills of a container of known volume.

The water column was divided into four strata, and the inlet placed at the center of the stratum. The pump was brought to speed, the outlet hose inserted in the spinner, and the stratum sampled

for a 15-min interval. After 15 min the outlet hose was quickly withdrawn, the pump speed reduced, and the hose inlet lowered to the next stratum for 5 min of flushing before the next 15-min sample was taken. The four strata were therefore sampled in a 75-min pumping series which was initiated every 2 h and continued for 24-36 h.

At the same time that the pump inlet was being deployed astern on the main wire, a Lerici current meter (Frassetto 1967), modified for deck readout of current velocity, was deployed amidship on the hydrographic wire. Fifteen-minute records at each depth stratum were obtained simultaneously with plankton samples. All current meter records were annotated on a strip chart recorder in the deck readout unit.

To link the vertical distribution of the shrimp larvae to the current vectors at depth, the median level of larval vertical distribution was calculated (Cronin and Forward 1979) for each of the larval substages at each 4-h time interval and assigned to one of the four depth strata. The intermediate (2-h) larval distributions were interpolated from the 4-h time series. The current vectors for each 2-h time interval, associated with the depth stratum (levels 1-4) to which the median larval depth corresponded, were added progressively over 24 h for each larval substage (Fig. 7b, c). In addition to the median larva, three other hypothetical behavior patterns were modelled: 1) a nonmigratory surface dwelling animal; 2) a nonmigratory near-bottom dwelling animal; and 3) a larva (12:12 larva, Figs. 7, 8, 9) that followed the behavior pattern dictated by Penn's (1975) hypothesis, i.e., it moved the full height of the water column on a strict 12:12 day: night cycle for the entire length of the larval life.

A photometer, with both deck and submersible cells, was used to measure the ambient and submarine irradiance ($\mu W/cm^2$). Irradiance levels were recorded at 2 m intervals at the start of every 2-h pumping series during daylight. The meter was not sensitive enough to record variable levels of moonlight or starlight. Temperature profiles were obtained with both a bathythermograph and water sampled from the pump outlet.

Plankton biomass (settled volume) from discrete depth samples was obtained by settling the fixed sample (10% formaldehyde, sodium tetraborate buffer) for 4 h in Imhoff cones (Rothlisberg and Jackson 1982). The samples were then transferred to 2% 2-phenoxy ethanol for preservation and subsequent microscopic examination. For economy and expediency, only every other sampling series (4-h) was examined. No subsampling scheme was employed. Numbers of larvae in each sample were standardized to numbers per cubic meter based on the calibrated pumping rates.

RESULTS

Ontogeny of Vertical Migration

From sampling done on 22 and 23 March 1977 north of Groote Eylandt (Station 210), early larvae (zoeal stages 1-3) were seen to move up into the water column only at night (Fig. 3). This movement was very limited and rarely extended more than one-half the distance to the surface. By day they were almost totally restricted to the bottom stratum of the water column sampled. The mysis stages extended the range of their nighttime excursions to the full water column without completely abandoning the lower part of the water column at night. They too returned almost completely to the bottom stratum by day. Postlarval numbers in the samples were too few to make generalizations, but they did appear to

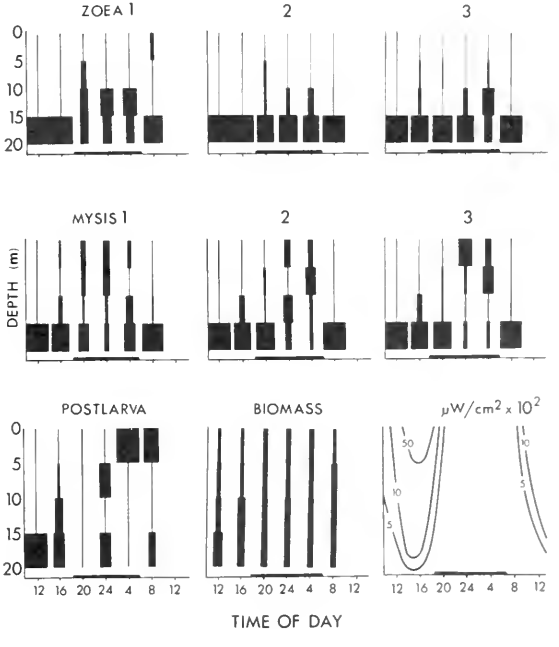

FIGURE 3.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance ($\mu W/cm^2$) for 22-23 March 1977 at Station 210 north of Groote Eylandt. The dark horizontal bar indicates night.

extend the mysis pattern further by almost completely abandoning the lower parts of the water column by night but still returning by day.

Variations in the Pattern of Vertical Distribution

High light penetration was characteristic of the station occupied on 22 and 23 March 1977 (Fig. 3). Conditions were calm, isothermal, and clear with a secchi disc depth of 16 m in the 22 m water column and penetration of the 1,000 μW/cm^2 isolume to 20 m. Under these conditions, movement of the larvae away from the deepest stratum occurred only at night and almost all stages (first zoea (Z1) through third mysis (M3)) returned to the bottom stratum during daylight.

On 6 and 7 May 1977 (Station 310), though sea state and wind conditions were comparable with the previous sampling session, increased turbidity limited the 1,000 μW/cm^2 isolume penetration to only 10 m or about half of the water column (Fig. 4). This change in light penetration paralleled marked changes in the vertical distribution of all larval stages. During daylight, early larval stages (zoea 1-3) were not confined to the bottom stratum. The day-night differences in vertical distribution, though present, were less distinct than in the previous case, and these early larval stages were seen even at the surface at night. The day-night pattern for mysis stage larvae was even less distinct. Though spread throughout the water column, they appeared to be slightly more concentrated at or near the surface at night. Postlarval (PL) numbers were again low, and they were near the surface during the entire diel period. They were more abundant in the surface stratum during the night.

At the station east of Mornington Island on 27 and 28 March 1977 (Station 270) the wind and sea conditions were extremely calm but light penetration was even more diminished than in the previous two cases. On this occasion the 1,000 μW/cm^2 isolume penetrated only about one-third of the water column (Fig. 5). Further changes in the patterns of larval distribution were seen. Early larval stages were concentrated in the middle two depth strata with nighttime movements to the surface. The mysis stage larvae were also predominantly in the middle part of

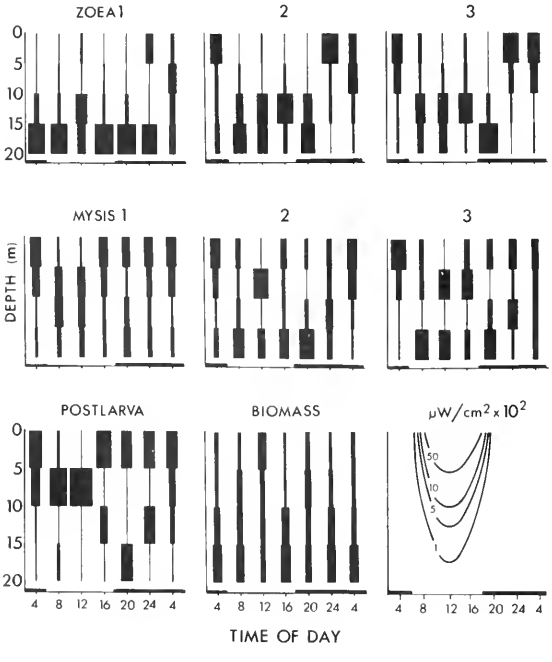

FIGURE 4.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance (μW/cm^2) for 6-7 May 1977 at Station 310 north of Groote Eylandt. The dark horizontal bar indicates night.

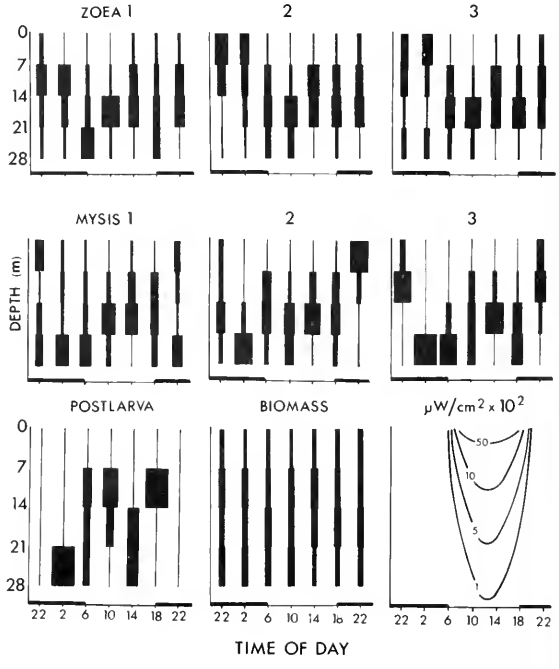

FIGURE 5.—Relative larval abundance (percent) by substage and depth stratum, vertical distribution of settled plankton volume (percent), and vertical profiles of submarine irradiance (μW/cm^2) for 27-28 March 1977 at Station 270 east of Mornington Island. The dark horizontal bar indicates night.

the water column by day but spread out to both the surface and the bottom strata at night. Again the postlarval numbers were low and little day-night patterning was evident. No postlarvae were caught at any time in the surface stratum and were near the bottom both day and night.

Of concern was possible day-night variation in larval abundance due to avoidance of the inlet hose and/or larval distribution outside the range of the sampler. Of particular concern was the possibility that during the day larvae were on or near the bottom below the hose inlet at its lowest extent. To test statistically for a temporal variation in larval abundance, the larval numbers were initially combined over all depths within a sampling time interval and then a square root transformation was applied. A sine curve was fitted to estimate gradual rather than abrupt day-night changes in larval numbers. Postlarval numbers were too low to include in the analysis. Time alone was highly significant for the total number of larvae and significant at lower levels for three of six larval substages (Table 1). The high level of significance of the station-time interaction for all but the Z2 larvae indicates that the small diel variation in abundance was variable between sampling occasions. Inspection of the data showed that the peak abundances varied by stage, location, and time of day and that there was no systematic difference in catchability which would bias the interpretation of the diurnal patterns shown previously.

To add confidence to the diagrammatic interpretation (Figs. 3-5), further analysis, using an arc-sine transformation of the proportional larval abundances by depth also, showed that the abundances at the four depth strata were quite variable from one date to the next. This was indicated by the high degree of significance of the station effects at almost all depths (Table 2). The abundances of larvae in the surface stratum (level 1) showed the most consistent relationship with time of day, with larvae rarely at the surface by day, on any cruise, and increasing in abundance at the surface by night. Further, the station-time interaction at depth (e.g., level 3) was significant for most larval stages and substages, indicating a high degree of station-to-station variation in the depth of peak abundance.

TABLE 1.—Summary of analysis of variance of larval abundance. A square root transformation was applied to all data pooled within each time increment over all four depths.

Stage/ substage	F-ratios: Station (2, 11 df)	Time (2, 11 df)	Station-time interaction (4, 11 df)	Error mean square
Zoea	9.98**	4.92*	4.89*	2.6519
Mysis	32.04***	3.58+	4.82*	1.6531
Total	56.63***	18.03***	10.75***	1.0528
Z1	6.21*	1.98	6.31**	0.8505
Z2	11.86**	4.86*	2.89+	1.4859
Z3	11.49**	4.81*	8.33**	1.0520
M1	33.30***	2.94+	3.49*	1.8837
M2	25.72***	1.66	13.65***	0.2452
M3	40.68***	0.13	12.88***	0.2976

***$P<0.001$, **$P<0.01$, *$P<0.05$, + $0.05<P<0.10$.

TABLE 2.—Summary of analysis of variance of proportional larval abundance at four discrete depths. An arc-sine transformation was applied to the percentages.

Stage/ sub-stage	Level	F-ratios: Station (2, 11 df)	Time (2, 11 df)	Station-time interaction (4, 11 df)	Error mean square
Zoea	1	7.53**	5.29*	2.56+	0.03293
	2	17.01***	0.72	2.15	0.02167
	3	4.56*	0.60	6.49**	0.02906
	4	22.68***	2.31	2.10	0.04125
Mysis	1	7.33*	16.11***	0.76	0.02179
	2	10.55**	1.94	8.46**	0.01277
	3	7.68**	2.58	3.35+	0.01925
	4	14.89***	1.25	9.27**	0.03075
Z1	1	1.25	0.13	2.10	0.03876
	2	10.61**	0.78	0.91	0.04839
	3	3.84+	0.59	7.31**	0.03953
	4	12.74**	2.12	3.27+	0.05937
Z2	1	6.65*	7.42**	2.23	0.04838
	2	17.53**	0.46	1.59	0.02760
	3	8.85**	1.03	5.56*	0.03270
	4	30.46***	3.48+	0.97	0.05877
Z3	1	11.05**	6.43*	2.38	0.3573
	2	9.99**	0.27	1.09	0.03112
	3	4.03*	1.89	4.10*	0.04522
	4	14.00***	0.47	1.22	0.09720
M1	1	9.13**	16.15**	0.35	0.01989
	2	13.82***	0.27	5.78**	0.01714
	3	4.26*	1.90	3.39*	0.02365
	4	40.92***	2.24	21.86***	0.01289
M2	1	2.50	4.97*	1.11	0.06961
	2	2.06	0.34	1.07	0.08163
	3	3.31+	0.20	3.02+	0.05118
	4	5.70*	1.06	2.44	0.10437
M3	1	4.85*	9.31**	0.80	0.05065
	2	1.21	0.16	2.27	0.09051
	3	3.74+	1.01	9.24**	0.03211
	4	2.22	1.51	2.13	0.16646

***$P<0.001$, **$P<0.01$, *$P<0.05$, + $0.05<P<0.10$.

Consequences of Vertical Migration

At the two sampling locations in the Gulf of Carpentaria, the currents were dominated by a tidal component as seen in the individual current vectors, represented by the mean speed and direction for the 15-min sampling periods (Fig. 6). Detailed analyses of these records, however, were complicated by three factors: 1) time lag between sampling surface and bottom strata; 2) short-term wind events; and 3) anomalous current vectors at depth. At most sampling times,

current speed and direction changed with depth. Although the speed usually decreased with depth (e.g., Fig. 6a, 0200; 6c, 2200), an increase was noted on some occasions, especially around the time of slack water (e.g., Fig. 6a, 1200; 6b, 0000). This apparent increase is believed to be an artifact of the time lag in sampling with the migrating current meter. Short-term wind events can also be detected at the surface stratum (Fig. 6b, 2.5 m; 1800-2200). Time lag and wind events alone, however, cannot explain all the variation in the current vectors. Other anomalous current vectors at depth (e.g., Fig. 6a, 1000, 17.5 m; 0800, 7.5 m) represent short-term nontidal perturbations of unknown origin.

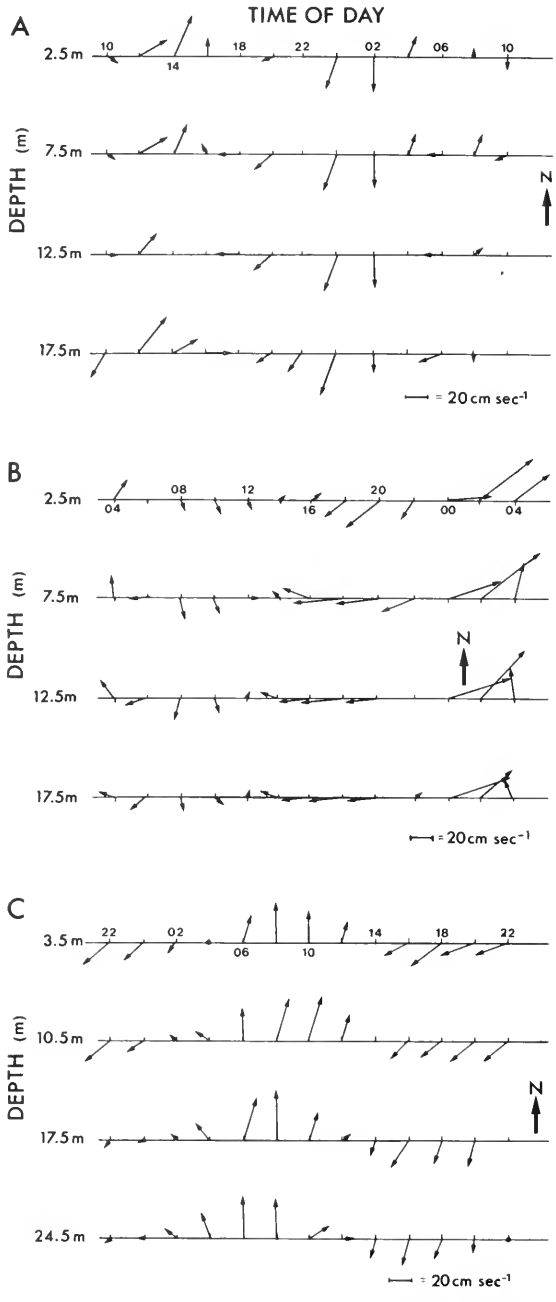

FIGURE 6.—Mean 2-h current vectors at four depths and three stations: A) Station 210, 22-23 March 1977 north of Groote Eylandt; B) Station 310, 6-7 May 1977 north of Groote Eylandt; C) Station 270, 27-28 March 1977 east of Mornington Island.

Over the 24-h sampling period at Station 210, the net displacement (measured as a straight line from the origin to the end of the progressive vector) was quite variable for migratory and nonmigratory animals. Surface-dwelling animals would have been displaced to the northwest, near-bottom dwelling ones to the south, and the 12:12 larva almost due west. The net drift of the 12:12 larva was considerably less than either of the nonmigratory animals. The larval movements (Fig. 7b, c) based on sampled vertical distributions would have closely paralleled the bottom currents in this case because so much of their time was spent in the lower parts of the water column. The slight differences in displacement direction and distance between substages reflect the differences in depth distribution. Because of their wider excursions, the postlarvae were exposed to more of a mixture of the bottom and surface currents and therefore approached the 12:12 larva in direction of advection during that larval stage. To calculate an approximate total displacement over the whole of the larval phase, the 24-h picture was extrapolated by making several assumptions. Firstly, the larval life span was set at 14 d with 2 d for each larval substage (Z1, Z2, Z3, M1, M2, M3, PL). Secondly, within each substage the same vertical migratory behavior prevailed on both days. Thirdly, the current regime, seen during the 24-h sampling period, was constant over the 14-d larval life. By doubling the length of the daily resultant vectors for each larval substage and adding them progressively, the 2-wk displacement is approximated (Fig. 7d). The calculation of absolute distances is not precise because of the nature of the assumptions, especially the third. The period of sampling was, however, between neap and spring tides so the tidal currents would have been moderate and a reasonable approximation of mean velocities over the tidal cycle. Under these criteria, the median larva would have been displaced about 69 km (37 nmi), the 12:12 larva 25 km (13 nmi),

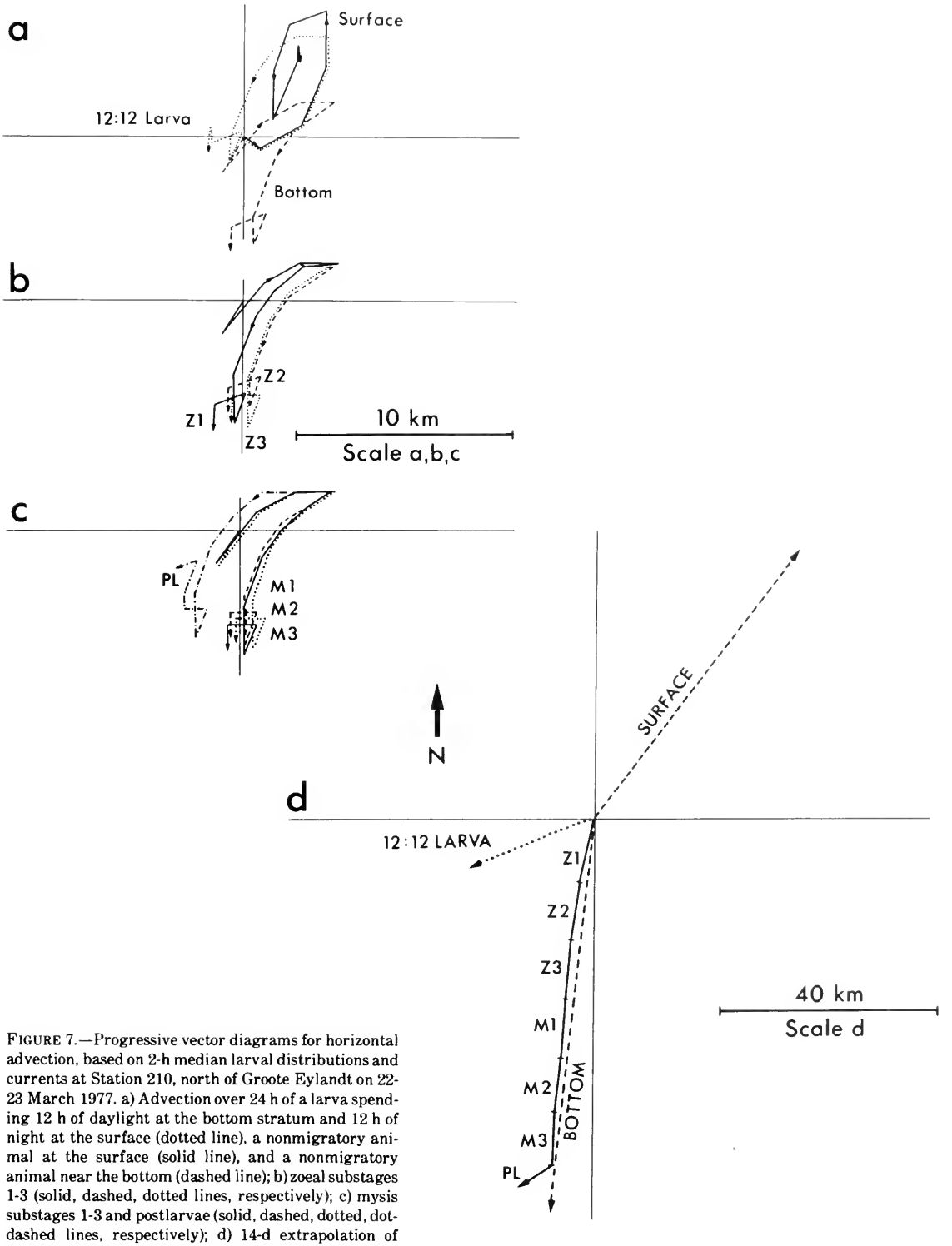

FIGURE 7.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 210, north of Groote Eylandt on 22-23 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

and the surface and near bottom nonmigratory animals 62 km (34 nmi) and 72 km (39 nmi), respectively. The larvae were displaced to the southwest from the sampling station north of Groote Eylandt. This trajectory would have taken them in the general direction of Groote Eylandt or the coastal rivers in the Limmen Bight, southwest of Groote Eylandt. Greater distances could be attained if the pelagic postlarval stage was maintained through several instars before metamorphosing to the benthic-living juvenile shrimp.

Procedures for approximating displacement distance and direction on the other two sampling occasions were similar but the resultant displacements were quite different because of the different vertical distribution patterns seen on each occasion. At Station 310, north of Groote Eylandt, submarine irradiance was reduced and the vertical distribution of the larval substages was more varied (Fig. 4). Consequently, the horizontal displacements of individual larval substages (Fig. 8b, c), though dominated by the bottom currents (Fig. 6b), were quite varied. The hypothetical 2-wk displacement was again in the same direction as the bottom current (Fig. 8d), but the distance was enhanced by the fact that larvae were further off the bottom in their nightly excursions for slightly higher proportions of the time. Total horizontal displacement over the 2-wk larval period, up to and including 2 d of postlarval life, would be about 75 km (40 nmi). The direction of advection of the median larva in this case is to the northwest. The 12:12 larva would have been displaced seawards to the central Gulf of Carpentaria.

Analysis of the larval migratory patterns (Fig. 5) and the current regime (Fig. 6c) at Station 270 east of Mornington Island showed yet another pattern of displacement (Fig. 9). Here, because there were large numbers of larvae in the upper part of the water column both night and day, the displacement would have been in the direction of the surface currents (Fig. 9a, b, c). Slight deflection away from the surface direction was seen in older larvae (M1-PL) as more of them moved into the lower part of the water column (Fig. 9d). The displacement distance over the 2-wk period would have been 98 km (53 nmi). All advection was to the west, with the 12:12 larva going to the southwest towards the coast and the median larva heading west-northwest, away from the coast, in the general direction of the surface currents.

DISCUSSION

While it is widely thought that changes in light intensity are the primary environmental cues that initiate and control the diel vertical migrations in aquatic animals (Ringelberg 1964; Thorson 1964; Boden and Kampa 1967; Hutchinson 1967; Segal 1970; Buchanan and Haney 1980), there have been cases in which the timing of the migration was not strictly in phase with changes in light intensity, possibly because of changes in subsurface light and/or feeding history and strategy of the animals (Enright and Honegger 1977; Bohrer 1980). In shallow-water coastal environments, factors affecting light penetration and therefore vertical distribution of animals are numerous and subject to rapid change. Turbulence with concomitant turbidity caused by both wind and tidally induced currents, river and coastal runoff, and rapid phytoplankton growth would be the more significant causes of light reduction. It is these short-term changes in submarine irradiance that are probably responsible for some of the conflicting reports about whether or not penaeid larvae migrate vertically.

The first mention of differential vertical distribution of penaeid larvae is by Racek (1959), sampling off the eastern Australian coast. His sampling was not strictly stratified, he published no supportive data, and the conclusions are probably drawn from a combination of field and laboratory observations. He stated that nauplii as well as first and second protozoeae (= zoeae) were strongly attracted to bright light. I saw no evidence of this in our field collections but have observed it under artificially high light intensities in the laboratory. There may be some threshold light intensity at which point penaeid larvae shift their behavior from photonegative to photopositive similar to that described for the larvae of *Uca pugilator* (Herrnkind 1968). From his field sampling, Racek found that late protozoeae and early mysis stages rose to the surface at night and sunk to lower strata during daylight. The vertical distribution of late mysis and postlarvae were not mentioned in Racek's brief account.

In the study by Eldred et al. (1965), the day-night pattern of vertical distribution was neither persistent within nor consistent among genera. For *Penaeus duorarum* only postlarvae were discussed. Pooled samples were dealt with, so little information about station-to-station variation

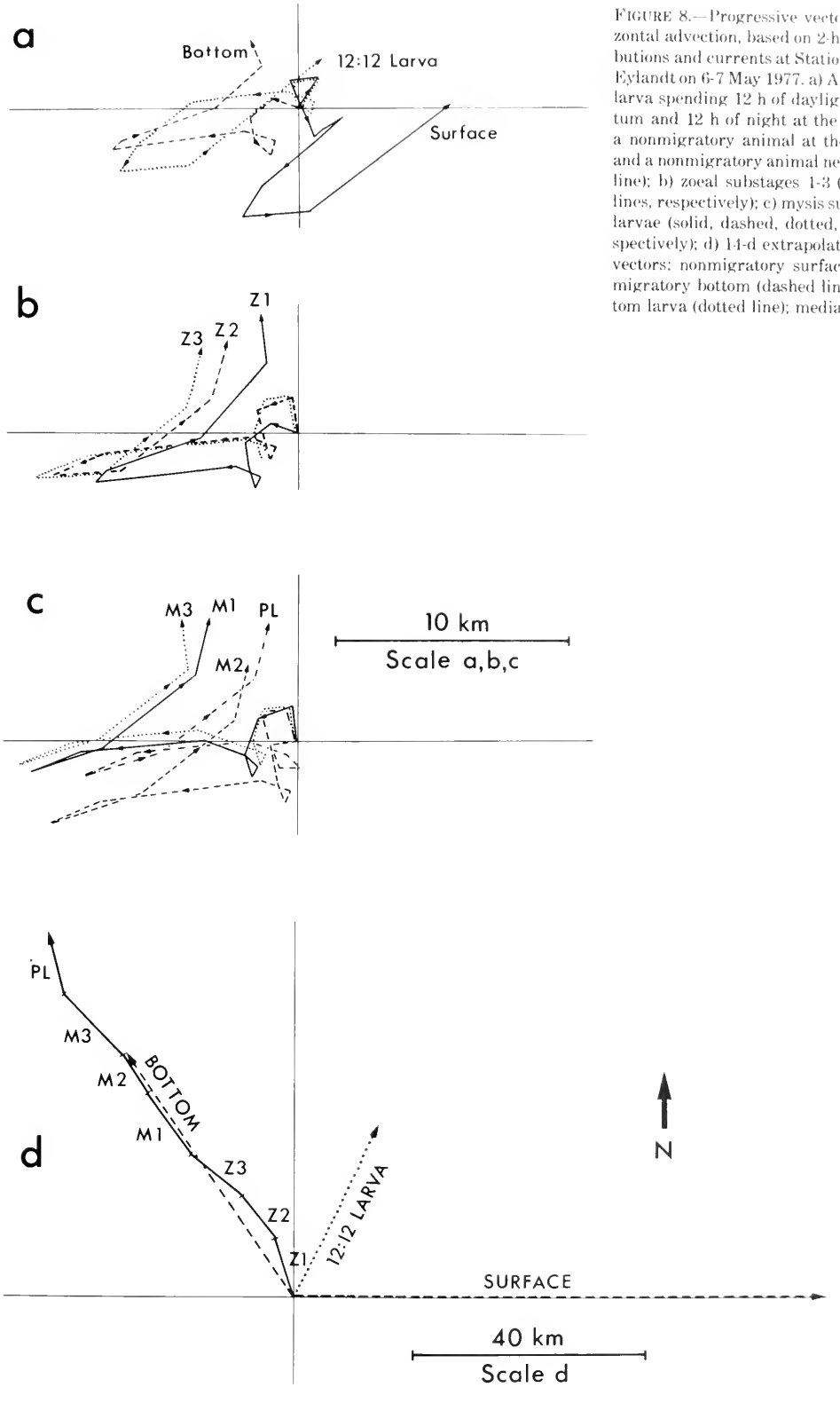

FIGURE 8.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 310, north of Groote Eylandt on 6-7 May 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

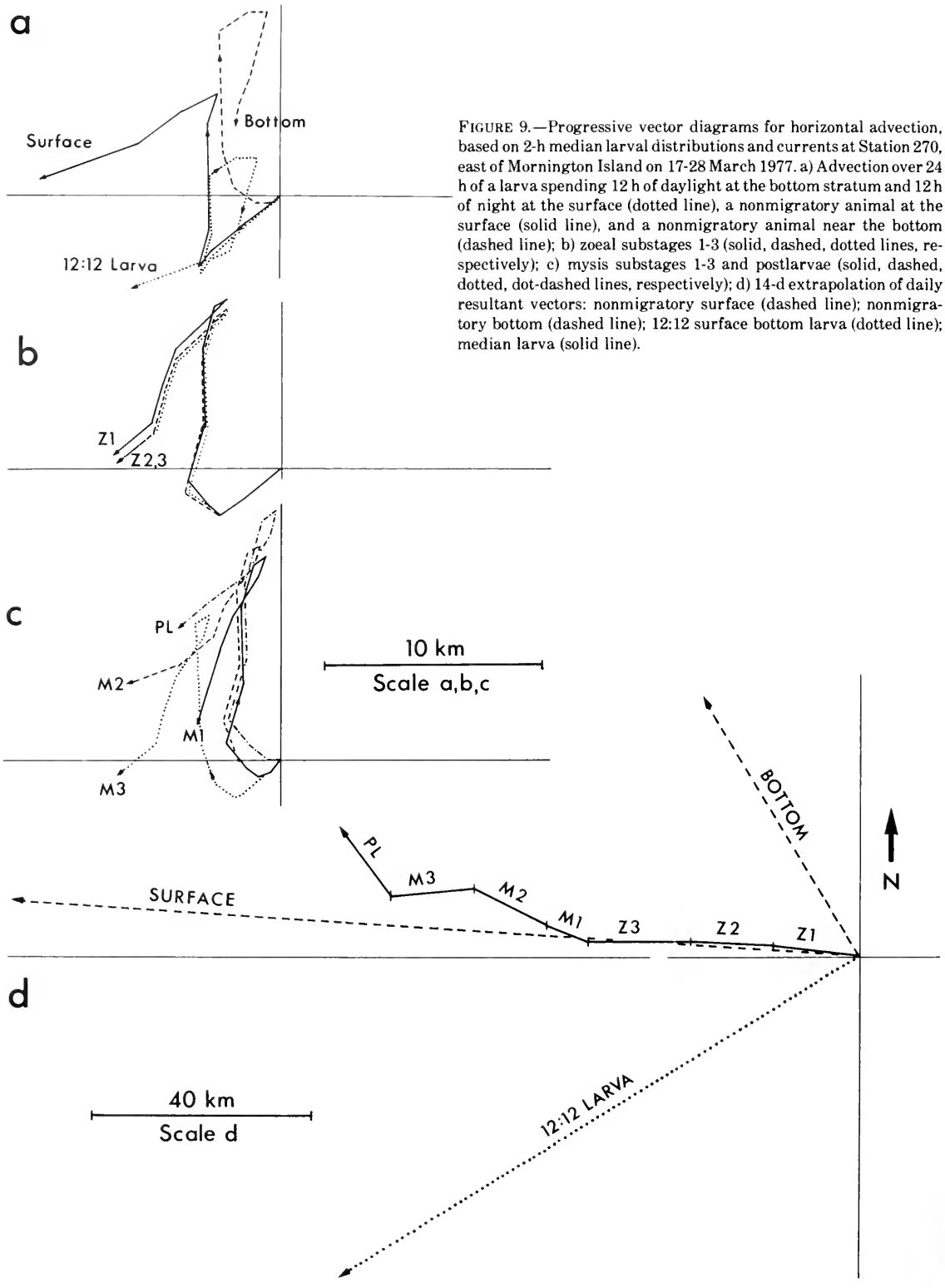

FIGURE 9.—Progressive vector diagrams for horizontal advection, based on 2-h median larval distributions and currents at Station 270, east of Mornington Island on 17-28 March 1977. a) Advection over 24 h of a larva spending 12 h of daylight at the bottom stratum and 12 h of night at the surface (dotted line), a nonmigratory animal at the surface (solid line), and a nonmigratory animal near the bottom (dashed line); b) zoeal substages 1-3 (solid, dashed, dotted lines, respectively); c) mysis substages 1-3 and postlarvae (solid, dashed, dotted, dot-dashed lines, respectively); d) 14-d extrapolation of daily resultant vectors: nonmigratory surface (dashed line); nonmigratory bottom (dashed line); 12:12 surface bottom larva (dotted line); median larva (solid line).

can be obtained. The broad picture based on percentages indicated that more postlarvae occurred at the surface than near the bottom during daylight while more were near the bottom at night. The actual locations were not given but were probably pooled observations of a number of nearshore stations. Thus, the possibility exists that these postlarvae, close to nearshore nursery grounds and sampled mostly on flood tides, were in a tidally induced behavior pattern that has been shown for the postlarvae of *P. duorarum* (Hughes 1969a, b), *P. aztecus* (St. Amant et al. 1966), *P. plebejus* (Young and Carpenter 1977), and *P. merguiensis* (Munro 1975; Staples 1980). The zoeal and mysis-stage larvae of *Trachypenaeus* and *Sicyonia* were also sampled in the Eldred et al. (1965) study. These early larvae (all stages pooled) showed a marked increase in abundance near the bottom during the day and slightly increased abundances at the surface at night. In their summaries, no larval distributions with intermediate depths and times were shown. In the Gulf of Carpentaria there are at least eight genera represented: *Penaeus, Metapenaeus, Atypopenaeus, Parapenaeopsis, Trachypenaeus, Metapenaeopsis, Solenocera,* and *Eusicyonia.* When generic resolution was applied to the present series of samples, no changes in the patterns emerged, but the numbers of larvae available for each analysis decreased. It therefore seemed reasonable to analyze the pooled samples since it appeared the behavioral patterns were family-wide.

Temple and Fischer (1965) were the first to show clear patterns of vertical distribution by penaeid larvae. They too were sampling mixed genera of penaeids (*Penaeus, Trachypenaeus, Sicyonia,* and *Solenocera*). Using discrete depth sampling nets, they showed some increase in migratory ability with the development of the larval stages, as well as the variable patterns seen on different sampling occasions. They did not measure light penetration and attributed the variations of larval distribution to differing conditions of water column structure and stability, as characterized by the presence or absence of a thermocline. The same degree of variation in vertical migratory patterns was seen in this study under isothermal conditions, in calm to slight seas. Therefore, turbulence seemed to be of minimal importance in explaining the differences in distribution patterns. However, even under near uniform wind and sea conditions, light penetration in the shallow coastal stations was quite variable and this variation was reflected in larval behavior. It therefore appears that light penetration is the dominant environmental variable affecting larval behavior. There is little doubt, under conditions of strong vertical mixing in shallow water, that both turbulence and the concomitant increase in turbidity would result in a mixed vertical distribution. Temple and Fischer (1965) also believed that there was evidence for a reversal of vertical distribution with growth from zoeal to postlarval stage. Their summary figure (fig. 3, p. 62) is not convincing and again may be biased by the change in behavior of postlarvae to a tidally dominated one used to enter coastal estuaries (Temple and Fischer 1965). In the Gulf of Carpentaria sampling, there was no evidence of a reversal with development, but these samples were taken well offshore so a tidal-coastal behavior pattern cued by salinity or pressure differences was probably not in evidence.

Only one other study of larval penaeid vertical migration has been undertaken; Jones et al. (1970) sampled *P. duorarum* larvae off southern Florida. Summary figures of pooled data also show the ontogenetic change in vertical migratory ability of the larvae, as well as variability in the patterns between sampling periods. No environmental data are provided to help explain the difference.

All these studies (Racek 1959; Eldred et al. 1965; Temple and Fischer 1965; Jones et al. 1970) were undertaken to help explain how the vertical distribution of penaeid larvae affects dispersal from offshore spawning grounds to nearshore or estuarine nursery grounds. None of the studies, however, was able to explain the variable results encountered, and furthermore, the currents that would be responsible for this onshore movement were not measured. Penn (1975) attempted to overcome these deficiencies by using an idealized larval behavior, one which required all larvae to move the full height of the water column from the surface to the bottom on a strict night-day cycle (12:12 larva in Figs. 7, 8, 9). This, however, did not allow for differential larval abilities and/or environmentally induced variations in behavior. Furthermore, because of the lack of in situ current recordings, he used differences in predicted tide heights to calculate residual flows. Penn found, even with these constraints, a general mechanism by which larvae could be transported farther inshore at night than offshore during the day, against the prevailing cur-

rents between March and August, the main period of postlarval recruitment in Shark Bay, Western Australia. Penn proposed that during a larval life lasting 2-4 wk the larvae would be displaced 30-80 km before becoming postlarvae at which time they would migrate more actively using a tidal cue. In the present study the 12:12 larva that behaved in a manner dictated by Penn's (1975) scheme seldom travelled in the same direction or distance as the median larva (Figs. 7, 8, 9). This is largely because these larvae did not utilize the full water column over all their larval life even under ideal conditions and that subtle changes in environmental factors changed the patterns of vertical distribution of all larval stages quite markedly.

With more detailed information on larval distribution and its causes, realistic dispersal distances and directions are even more dependent upon detailed knowledge of current speeds and direction at depth. In the present study there were shortcomings in assessing both short-term and long-term in situ current regimes. The migratory current meter used gave some indication of variation of speed and duration of currents but is probably biased by sampling technique and influenced, at times, by short-term wind events and short-term nontidal pertubations. Furthermore there were errors introduced by deploying the meter from a moored vessel. A certain amount of oscillation in current direction appeared during periods of low current velocity when the ship would swing on its anchor. This was overcome to some extent by using both a bow and stern anchor. The most serious shortcoming, however, is the robustness of the extrapolation from the 24-h record to the entire larval life of about 14 d. At best this would only be an approximation of the distance and direction of advection of median larva.

The distances estimated by extrapolation (ca. 70-100 km) are large enough to transport the larvae from the farthest known offshore commercial concentrations of adult penaeid shrimp in the Gulf of Carpentaria (Lucas et al. 1979) to their nearshore and estuarine nursery grounds. This range of advection is greater than that estimated by Penn (1975) even though in this study only a 2-wk larval life was used as opposed to a 4-wk period in his. The 2-wk period seems more realistic at ambient Gulf of Carpentaria temperatures (unpubl. data; Cook and Murphy 1969; Mock and Murphy 1971). This period still allows for one to two postlarval intermolts before settlement. It is suggested that the advection of the larvae limits the offshore adult distribution of those species of penaeid shrimp in the Gulf of Carpentaria that rely on nearshore or estuarine habitats for juvenile nursery grounds. There are no apparent depth or substrate limitations that would restrict the adult distribution to a coastal zone <100 km wide.

Whether or not differential larval advection can account for the large-scale temporal and spatial patterns of postlarval recruitment seen in the Gulf of Carpentaria (Staples 1979) is still open to speculation. There is some evidence from this study of offshore transport of larvae in March (Fig. 9d) at a time when large numbers of ripe female shrimp are present in the commercial fishery in the southeastern corner of the Gulf of Carpentaria. It may be this offshore advection of larvae that explains the subsequent low level of postlarval recruitment in the following weeks into the coastal rivers of this region of the Gulf of Carpentaria (Staples 1980). The short-term sampling of currents in the present study is not capable of annotating the long-term seasonal effects of tropical wind regimes and the long-term progression of tidal phase. Long-term monitoring and modelling of tidal and wind driven currents (Church and Forbes 1981; Forbes and Church in press) in the Gulf of Carpentaria has recently been completed and will be used to overcome this shortcoming of the present study. It is also likely that a better understanding of short-term meteorological events at critical times in the larval life history would help explain the year-to-year variation seen in the strength of postlarval recruitment in individual rivers around the gulf (Staples 1979) and the subsequent commercial catch (Lucas et al. 1979).

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FEEDING ECOLOGY OF 0-AGE FLATFISHES AT A NURSERY GROUND ON THE OREGON COAST

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ABSTRACT

The food habits of 0-age English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*; were investigated over a 2½-year period at a shallow nursery area (9-30 m) off the central Oregon coast. A total of 422 guts from recently metamorphosed fish (17-88 mm SL) were examined; only 16 were empty (4%). The greatest similarity in diets was between English and butter soles. Both species were benthophagous, feeding on a wide variety of prey, including palps of the polychaete *Magelona saceulata*, juvenile bivalves, siphons from tellinid clams, harpacticoid copepods, amphipods, cumaceans, and juvenile decapods. Speckled sanddabs fed equally on benthic prey (amphipods, cumaceans, decapods) and mysids, while sand sole almost exclusively ate mysids. The guts of all four species tended to be <25% full in the morning before 0900 h; stomach fullness gradually increased during the late morning and afternoon.

Food habits of English sole were a function of location of capture within the study area, season, and fish length. Juveniles <35 mm SL fed on small prey, e.g., polychaete palps, juvenile bivalves, tellinid clams, and harpacticoids, while larger individuals fed on larger prey, e.g., amphipods, cumaceans, and decapods. Diets of English sole <35 mm SL varied greatly both between seasons in the same year and between years. Spatially, the diets of English sole captured in trawls at the same depth and different depths were similar in January 1979 but highly variable in May 1979. These temporal and spatial differences in feeding are probably caused by seasonal changes in the abundance and spatial distributions of benthic prey.

Many juvenile flatfishes recruit to the sea floor in well-defined nursery areas following metamorphosis from pelagic larvae. The types and densities of food items present in such benthic regions potentially can affect growth and mortality of recently settled flatfish species (Paloheimo and Dickie 1966; Steele et al. 1970; Cushing and Harris 1973). In addition, whenever the nursery grounds of several species coincide or overlap, interspecific interactions originating from similarities in diet may also be a factor regulating growth and survival (e.g., Edwards and Steele 1968). Four species of pleuronectiform fishes—English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*—utilize the shallow water of the open Oregon coast as a site of benthic recruitment and early growth. All but *C. stigmaeus* are important to the Oregon trawl fishery. English sole ranks among the top three commercial species based on annual landings.

In conjunction with a long-term research program designed to improve management of Oregon's multispecies demersal fishery (Pearcy et al. 1977; Richardson and Pearcy 1977; Pearcy and Hancock 1978; Laroche and Richardson 1979; Hayman and Tyler 1980), we examined the prey selected by recently settled individuals of these four species at one site over a 2½-yr period. Our specific goals were to describe the food habits of these fishes, to relate the temporal and spatial variability of the English sole diet to changes in prey abundance and distributions, and finally to compare the dietary and habitat overlap of English and butter soles.

MATERIALS AND METHODS

The area selected for this work was located off Moolach Beach on the open Oregon coast (Fig. 1). Situated between Yaquina Head and Cape Foulweather 10 km north of the nearest estuary, this site has been the focus of recent work on the recruitment and growth of juvenile pleuronectids (Laroche and Holton 1979; Rosenberg 1981; Krygier and Pearcy[2]) and the food habits of adult

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[2]Krygier, E., and W. G. Pearcy. Distribution, abundance, and growth of 0-age English sole in estuaries and along the coast of Oregon: the importance of estuarine nursery grounds.

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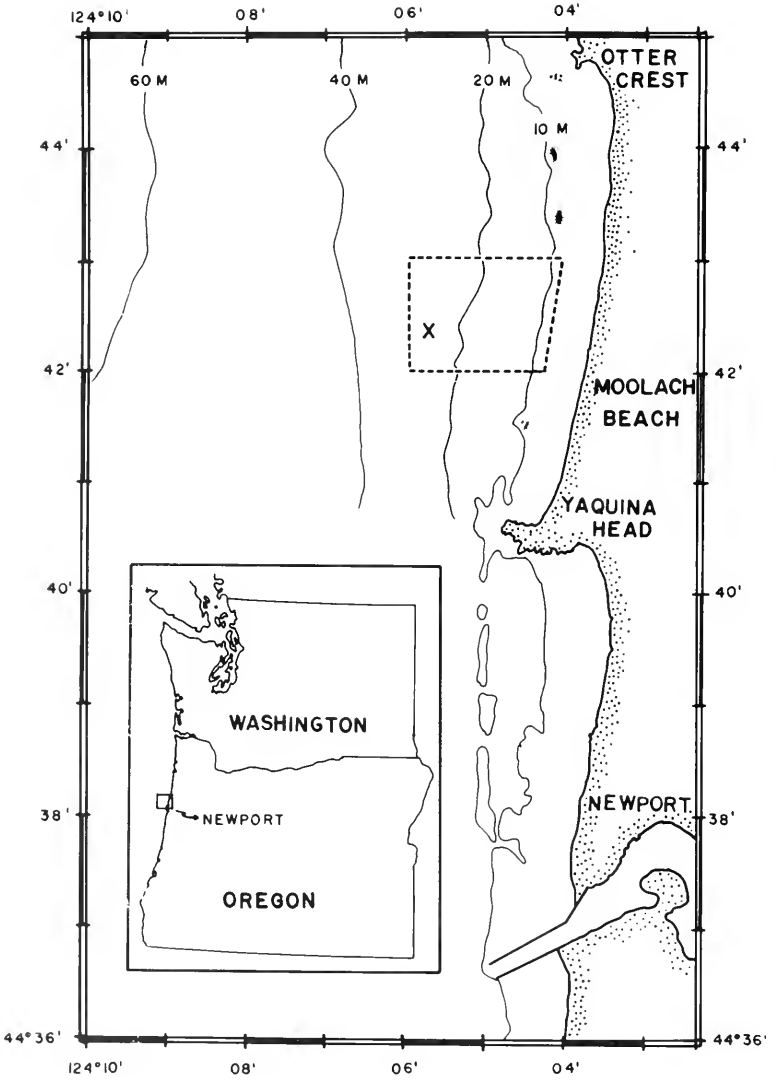

FIGURE 1.—Location of study area. Dotted lines enclose area from which beam trawl samples were collected; "X" marks location of box core and Smith-McIntyre grab samples.

flatfishes (Wakefield[3]). Trawl samples collected from this area between May 1977 and September 1979 were utilized for our work. A 1.5 m beam trawl fitted with a recording odometer wheel and a 7 mm stretch mesh liner was employed for all but one of these collections. On one occasion, 22 March 1979, we obtained samples using a small otter trawl which also had a 7 mm stretch mesh liner. On each sampling date, 10-min tows covering about 750 m^2 surface area were made at several depths between the 9 and 30 m isobaths (0.9 and 2.7 km offshore, respectively). Fish were preserved in 10% buffered Formalin[4] immediately upon collection. No regurgitation of gut contents was observed. The daily time of sampling varied between 0830 and 1800 h.

From the 85 trawl collections obtained during this 29-mo period, we selected 31 for examination. Several criteria were used in choosing these samples. In keeping with an overall goal of the Pleuronectid Project to obtain detailed informa-

Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

[3]W. W. Wakefield. Feeding ecology within an assemblage of benthic fishes on the Oregon Continental Shelf. Unpubl. manuscr. School of Oceanography, Oregon State University, Corvallis, OR 97331.

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

tion on the most important commercial species, emphasis was placed on those trawls which contained English sole. Priority was also given to using samples which were collected between July 1978 and September 1979, since quantitative meiobenthic samples were also gathered from the study area during that period. We used selected trawl collections from 1977 and 1978 to investigate the between-year repeatability of trends noted in the 1979 data. Finally, only hauls containing specimens 70 mm SL and less were used.

In the laboratory a size range of juvenile flatfish was selected from each of the trawls chosen for study. Standard length of each specimen was recorded prior to removal of the gut. Both the stomach and intestinal tract were removed and opened under a dissecting microscope; gut contents were identified to the lowest possible taxon and counted. We used a subjective scale ranging between 0 and 4 to quantify the degree of gut fullness (0 = <5% full, 1 = 5-25% full, 2 = 25-50% full, 3 = 50-75% full, 4 = 75-100% full).

Quantitative data for each prey category were summarized in two ways. The frequency of prey occurrence, expressing the proportion of all fish sampled which had a given food item in their gut, was computed for each flatfish species within a trawl. The mean percent composition, based on numerical abundance, was determined also by averaging the percent composition of each individual fish gut for a given species within a trawl. When more than one trawl was examined from a sampling date, the frequency of occurrence and percent composition from the separate trawls were averaged to give an overall mean. Diversity (H') of prey consumed was computed using natural logarithms (Pielou 1969).

On two sampling dates, 29 May and 30 June 1979, English sole were captured at the study site and returned live to the laboratory along with sand collected from the same area using a 0.25 m^2 box core. Fish were placed in aquaria with the sediments, and their behavior was monitored over several days while they fed on naturally occurring prey in the sediments. Fresh seawater (12°C) was circulating continually through each aquarium. A photoperiod matching that experienced by the fish in the field was maintained using room lighting.

Quantitative meiobenthic samples were obtained from the study area at one site in 25 m of water (Fig. 1). Three replicate 0.25 m^2 box cores, positioned 30 m apart, were collected on each of six cruises between July 1978 and May 1979. Box cores were subsampled with at least three randomly placed clear plastic cores (1.9 cm internal diameter) which were in turn vertically partitioned into six depth increments (0-1 cm, 1-3 cm, 3-6 cm, 6-11 cm, 11-18 cm, and >18 cm). These plastic corers were also used to subsample Smith-McIntyre grabs collected on two cruises in July and September 1979 at the same site. Samples were preserved in 10% buffered Formalin and stained with rose bengal. The fauna was extracted from the sediments (well-sorted fine sand) by shaking and decanting followed by three rinses. A 38.5 μm sieve was used to retain the fauna. Harpacticoid copepods and nematodes were identified to species and enumerated.

RESULTS

The data for all four flatfish species are summarized in Table 1. A total of 422 guts from recently settled fish (17-88 mm SL) were examined, only 16 of which were empty (4%). The guts of an additional 40 late stage IV and early stage V *P. vetulus* larvae (sensu Shelbourne 1957) were also examined. These metamorphosing individuals, ranging in size from 16 to 18 mm SL, all had empty stomachs and intestinal tracts.

The 13 prey categories identified (Table 1, top) were placed into three broad groupings based on the size of individual food items and their typical location within the habitat. Small benthic prey were composed of palps from the surface deposit-feeding polychaete *Magelona sacculata*, juvenile bivalves (predominantly *Tellina modesta* and occasionally *Siliqua patula*), siphon tips cropped from tellinid clams, harpacticoid copepods (mainly *Halectinosoma* spp. and a few *Thompsonula hyaenae* and *Rhizothrix curvata*), free-living nematodes (*Theristus* sp. and *Mesacanthion* sp.), and tube feet from the sand dollar *Dendraster excentricus*. These food items were on the order of 0.5-1.5 mm long. Larger benthic prey were amphipods (predominantly *Ampelisca* spp. and *Eohaustoris* sp.), cumaceans, decapods (juvenile *Cancer magister*, pinnotherid crabs, and *Callianassa californiensis*), and polychaetes (*Nephtys* sp., *Glycinde armigera*, *Magelona sacculata*, *Thalenessa spinosa*, and *Spiophanes bombyx*). These prey were usually juveniles measuring 1.5-4 mm in their largest dimension. Species identifications were difficult for this latter group because of their immature status and tendency to fragment after being eaten. Examina-

TABLE 1.—Summary of data collected for English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, are the number of fish out of the total examined which had empty guts. The two values listed for each prey category are average

Species and date	No. tows examined	No. fish examined	Length range (mm)	Small benthic prey					
				Magelona palps	Juvenile bivalves	Tellinid siphons	Harpacticoid copepods	Nematodes	*Dendraster* tube feet
English sole									
12 May 1977	1	12 (1)	18-29	0.08 (0.64)	0.42 (0.91)	0.22 (0.73)	0.22 (0.82)	— (0.18)	
23 June 1977	1	16 (0)	19-48	0.01 (0.19)	— (0.19)	0.18 (0.56)	0.42 (0.69)	— (0.06)	
12 June 1978	1	3 (0)	22-24	0.04 (0.33)	0.88 (1.0)		0.04 (0.66)	0.02 (0.33)	
15 June 1978	1	5 (0)	20-25	0.59 (1.0)	0.17 (0.80)		0.14 (1.0)	0.05 (0.40)	
13 July 1978	2	14 (0)	19-46	0.46 (0.89)	0.24 (0.83)	0.08 (0.33)	0.18 (0.70)	— (0.06)	
25 July 1978	1	12 (0)	24-84	0.09 (0.75)	0.01 (0.08)		0.17 (0.42)	0.40 (0.67)	
5 Sept. 1978	1	3 (0)	45-58		1.0 (1.0)				
14 Nov. 1978	1	5 (0)	18-21	0.99 (1.0)					
23 Jan. 1979	4	24 (2)	17-34	0.72 (0.94)	0.05 (0.25)	— (0.06)	0.13 (0.52)		
22 Mar. 1979	2	20 (0)	19-35	0.02 (0.50)	0.80 (1.0)	0.02 (0.36)	0.14 (0.90)		
18 Apr. 1979	2	27 (1)	19-38	0.10 (0.50)	0.20 (0.73)	0.17 (0.61)	0.23 (0.67)	— (0.22)	
29 May 1979	4	37 (5)	18-42	0.07 (0.24)	0.20 (0.25)	0.24 (0.38)	0.20 (0.41)	0.05 (0.19)	
30 June 1979	2	23 (1)	18-61		0.01 (0.50)	— (0.09)	0.14 (0.75)		0.61 (0.75)
19 July 1979	3	10 (0)	27-62		0.20 (0.25)		0.30 (0.79)		
8 Aug. 1979	2	11 (0)	30-87		0.26 (0.19)	0.03 (0.06)	0.03 (0.19)		
24 Sept. 1979	2	13 (0)	46-82		0.02 (0.07)		0.10 (0.35)		
Total		235 (10)							
$\bar{x}$ 1979				0.11 (0.27)	0.22 (0.41)	0.06 (0.20)	0.16 (0.57)	0.01 (0.05)	0.08 (0.09)
Butter sole									
23 June 1977	1	6 (1)	18-23	0.01 (0.20)		0.25 (0.80)	0.47 (0.80)		
15 June 1978	1	16 (0)	19-30	0.62 (0.87)	0.13 (0.60)	0.01 (0.13)	0.01 (0.27)	0.05 (0.47)	
25 July 1978	1	16 (0)	22-31	0.44 (0.75)	0.06 (0.12)		0.24 (0.82)	0.13 (0.57)	
29 May 1979	3	14 (2)	17-35	0.04 (0.10)	0.15 (0.50)	0.25 (0.62)	0.17 (0.63)	0.11 (0.25)	
30 May 1979	1	4 (0)	49-60		0.03 (0.25)		0.03 (0.25)		
19 July 1979	3	7 (0)	21-88	— (0.08)	0.38 (0.58)		0.11 (0.33)		
8 Aug. 1979	4	9 (1)	24-34	0.02 (0.38)	0.43 (0.50)	— (0.13)	0.47 (0.58)		
Total		72 (4)							
$\bar{x}$ 1979				0.02 (0.12)	0.25 (0.46)	0.06 (0.19)	0.20 (0.45)	0.03 (0.06)	
Speckled sanddab									
23 June 1977	1	4 (0)	34-44			0.41 (0.75)	0.13 (0.25)		
25 July 1978	1	5 (0)	41-65						
22 Mar. 1979	1	10 (0)	29-39		0.08 (0.10)	0.01 (0.10)	0.10 (0.10)		
18 Apr. 1979	1	10 (0)	29-38						
29 May 1979	2	14 (0)	33-50	0.13 (0.13)					
30 June 1979	1	7 (0)	30-52						
19 July 1979	2	11 (1)	35-70						
24 Sept. 1979	3	15 (0)	38-70						
Total		76 (1)							
$\bar{x}$ 1979				0.02 (0.02)	0.01 (0.02)	— (0.02)	0.02 (0.02)		
Sand sole									
22 Jan. 1979	2	6 (0)	30-38						
18 Apr. 1979	1	3 (0)	29-55						
19 July 1979	2	6 (0)	29-50						
8 Aug. 1979	2	13 (0)	31-52						
24 Sept. 1979	2	11 (1)	30-48						
Total		39 (1)							
$\bar{x}$ 1979									

tion of the meiofaunal cores revealed that all the organisms classified as "benthic" occurred in the upper 1 cm of sediment. Prey items which were never found in benthic samples were defined as "pelagic" and consisted of mysids (mainly *Neomysis kadiakensis*), calanoid copepods (*Pseudocalanus* sp.), and veliger larvae. This distinction between benthic and pelagic organisms is somewhat arbitrary, since some of these species are mobile epibenthic forms which probably occur both in the sediments and the overlying water.

Adequacy of the sample sizes used in determining food habits of the flatfish species was assessed using several techniques. The guts of 16 *Parophrys vetulus* (19-48 mm SL) and 16 *I. isolepis* (19-33 mm SL) were examined from each of two tows. These two species were selected because they fed on a much broader spectrum of prey than *Citharichthys stigmaeus* or *Psettichthys melanostictus* and hence are subject to greater sampling error. The cumulative number of prey categories encountered, expressed as a function of sample size, is shown in Figure 2. For both English sole and butter sole, after seven or eight fish had been examined, no new food categories were found. After examining only four fish, 75% of all food items had been collected. This qualitative consistency among guts is also reflected in the high frequency of occurrence (Table 1) for most prey. Quantitatively, the composition of gut

Citharichthys stigmaeus; and sand sole, *Psettichthys melanostictus*. Numbers in parentheses under the heading "No. fish examined" numerical percent composition and average frequency of occurrence (in parentheses). "—" indicates prey item <0.01.

Species and date	No. tows examined	No. fish examined	Length range (mm)	Large benthic prey				Pelagic prey		
				Amphipods	Cumacea	Decapods	Polychaetes	Mysids	Calanoid copepod	Veliger larvae
English sole										
12 May 1977	1	12 (1)	18-29	0.03 (0.27)		— (0.09)		0.01 (0.18)		
23 June 1977	1	16 (0)	19-48	0.15 (0.63)		0.24 (0.44)				
12 June 1978	1	3 (0)	22-24	0.01 (0.33)			0.01 (0.33)			
15 June 1978	1	5 (0)	20-25	0.02 (0.40)			0.04 (0.60)			
13 July 1978	2	14 (0)	19-46	0.02 (0.40)	0.01 (0.36)	0.02 (0.42)				
25 July 1978	1	12 (0)	24-84	0.18 (0.25)	0.04 (0.25)		0.03 (0.10)	0.04 (0.08)		
5 Sept. 1978	1	3 (0)	45-58							
14 Nov. 1978	1	5 (0)	18-21				0.01 (0.20)			
23 Jan. 1979	4	24 (2)	17-34	0.08 (0.52)	0.02 (0.14)			— (0.06)		
22 Mar. 1979	2	20 (0)	19-35	0.03 (0.60)	— (0.30)			— (0.10)		
18 Apr. 1979	2	27 (1)	19-38	0.25 (0.62)	0.04 (0.35)	— (0.03)		— (0.09)		
29 May 1979	4	37 (5)	18-42	0.03 (0.19)	0.03 (0.05)	0.17 (0.17)	0.02 (0.16)	— (0.13)		
30 June 1979	2	23 (1)	18-61	0.18 (0.54)	0.05 (0.25)	— (0.09)	— (0.09)			
19 July 1979	3	10 (0)	27-62	0.33 (0.70)	0.15 (0.50)	0.01 (0.08)				
8 Aug. 1979	2	11 (0)	30-87	0.45 (0.86)	0.21 (0.81)	0.01 (0.13)	— (0.33)	0.01 (0.06)		
24 Sept. 1979	2	13 (0)	46-82	0.29 (0.90)	0.41 (0.84)		0.18 (0.57)	— (0.09)		
Total		235 (10)								
$\bar{x}$ 1979				0.21 (0.62)	0.11 (0.41)	0.02 (0.06)	0.03 (0.14)	— (0.07)		
Butter sole										
23 June 1977	1	6 (1)	18-23	0.07 (0.80)				0.20 (0.20)		
15 June 1978	1	16 (0)	19-30	0.02 (0.33)	0.01 (0.20)		0.16 (0.87)			
25 July 1978	1	16 (0)	22-31	0.03 (0.25)	0.05 (0.38)		0.05 (0.38)	— (0.06)		
29 May 1979	3	14 (2)	17-35	0.04 (0.21)	0.03 (0.16)		0.03 (0.16)	0.05 (0.33)		
30 May 1979	1	4 (0)	49-60	0.32 (1.0)	0.26 (1.0)	0.29 (1.0)	0.07 (0.25)			
19 July 1979	3	7 (0)	21-88	0.21 (0.58)	0.04 (0.17)	0.18 (0.33)		0.08 (0.08)		
8 Aug. 1979	4	9 (1)	24-34	0.07 (0.54)	0.01 (0.63)			— (0.13)		
Total		72 (4)								
$\bar{x}$ 1979				0.16 (0.58)	0.09 (0.49)	0.12 (0.33)	0.03 (0.10)	0.03 (0.14)		
Speckled sanddab										
23 June 1977	1	4 (0)	34-44	0.20 (0.50)	0.13 (0.25)	0.11 (0.25)		0.03 (0.25)		
25 July 1978	1	5 (0)	41-65					1.0 (1.0)		
22 Mar. 1979	1	10 (0)	29-39	0.08 (0.30)	0.01 (0.10)			0.72 (0.80)		
18 Apr. 1979	1	10 (0)	29-38	0.20 (0.20)	0.52 (0.60)	0.03 (0.10)		0.25 (0.30)		
29 May 1979	2	14 (0)	33-50	0.25 (0.43)		0.30 (0.53)		0.32 (0.53)		
30 June 1979	1	7 (0)	30-52	0.03 (0.57)	— (0.05)	0.01 (0.29)		0.96 (1.0)		
19 July 1979	2	11 (1)	35-70	0.04 (0.20)				0.96 (1.0)		
24 Sept. 1979	3	15 (0)	38-70	0.14 (0.52)	0.08 (0.25)	0.20 (0.52)		0.59 (0.86)		
Total		76 (1)								
$\bar{x}$ 1979				0.12 (0.37)	0.10 (0.17)	0.09 (0.24)		0.63 (0.75)		
Sand sole										
22 Jan. 1979	2	6 (0)	30-38					1.0 (1.0)		
18 Apr. 1979	1	3 (0)	29-55					1.0 (1.0)		
19 July 1979	2	6 (0)	29-50					1.0 (1.0)		
8 Aug. 1979	2	13 (0)	31-52			0.03 (0.17)		— (0.13)	0.69 (0.80)	0.28 (0.40)
24 Sept. 1979	2	11 (1)	30-48					1.0 (1.0)		
Total		39 (1)								
$\bar{x}$ 1979						0.01 (0.03)		0.80 (0.83)	0.14 (0.13)	0.06 (0.08)

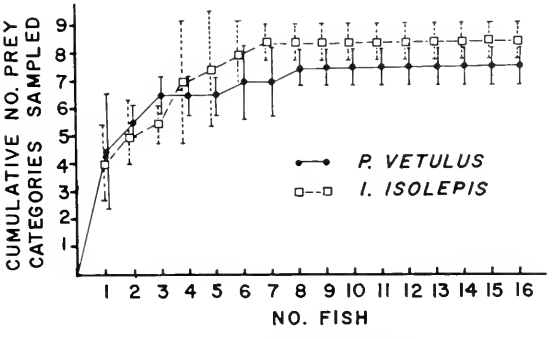

FIGURE 2.—Cumulative number of prey categories sampled as a function of sample size for *Parophrys vetulus* and *Isopsetta isolepis*. Each data point represents the mean of two separate trawl collections. Vertical bars are ±1 standard deviation.

contents varied little among individuals of a species within a trawl. For each species studied, food items from fish caught in the same trawl tended to have the same rank order of numerical abundance. This consistency of results was statistically significant; the null hypothesis of independence among prey rankings was rejected (Friedman's nonparametric randomized block ANOVA, $P<0.005$; Gibbons 1971). On several sampling dates the number of fishes available for study was small, e.g., *Parophrys vetulus* on 5 September 1978 (three fish), *I. isolepis* on 30 May 1979 (four fish). The small within-sample variability of these species, however, indicates that such small sample sizes will not unduly bias de-

termination of the major food items consumed.

As is apparent from Table 1, *P. vetulus* feeds on a wide variety of benthic animals. Juvenile bivalves, harpacticoid copepods, *Magelona* palps, and amphipods are particularly abundant in English sole guts. On most sampling dates, the frequency of occurrence of these four prey in the diet of English sole was high, although typically only one or two items dominated the diet numerically. Occasionally a food item which was usually rare became a major component in the guts of English sole, such as free-living nematodes on 25 July 1978 or echinoid tube feet on 30 June 1979. The diet of *I. isolepis* was very similar to that of *P. vetulus*, with the exception that butter sole fed to a greater extent on mysids and decapods. *Citharichthys stigmaeus* fed equally on large epibenthic crustaceans (amphipods, decapods, cumaceans) and pelagic prey. Polychaetes were totally lacking in the diet. *Psettichthys melanostictus* consumed mysids almost exclusively; only on 8 August 1979 were other pelagic prey found in the guts of this species. Average H' diversity of food consumed per sampling date in 1979 was 1.38 for English sole, 1.47 for butter sole, 0.81 for speckled sanddabs, and 0.14 for sand sole. The similarity in diets of these four species was compared by computing the percent similarity index (PSI; Whittaker 1960) based on the average 1979 proportions of prey consumed by each species (Table 2). Two of these paired comparisons, *Parophrys vetulus-I. isolepis* and *C. stigmaeus-Psettichthys melanostictus*, indicate similarities exceeding 50%. In the case of the speckled sanddab and the sand sole, this dietary overlap is based on their common utilization of one food category, mysids. English and butter soles share a wide variety of prey which were consumed in very similar proportions, e.g., 29 May 1979.

Observations of 20-25 mm *Parophrys vetulus* feeding in laboratory aquaria revealed two basic types of foraging behavior. In the first, fish remained motionless on the bottom and then periodically lunged forward 1-2 cm, striking at objects located on the surface of the sediment. In the second, fish slowly raised their heads above the bottom then rapidly thrust forward, causing the upper few millimeters of sediment to billow into suspension. *Parophrys vetulus* would then strike in rapid succession at small objects presumably temporarily displaced from the bottom. Neither type of behavior predominated; both were detected in all of the individuals observed. After monitoring these responses for several hours, fish were sacrificed and the guts examined. Harpacticoid copepods dominated the diet of these fish.

Shifts in prey preference as a function of fish size (age) were observed in English sole. The average diets of all *P. vetulus* less than and greater than 35 mm SL were computed using the 1979 data and then compared (Table 3). The dramatic difference in prey of these two size classes is apparent. Smaller fish (17-35 mm SL) consumed small prey almost exclusively, while larger fish (35-82 mm SL) only occasionally ingested these small items, choosing instead amphipods and cumaceans. *Isopsetta isolepis* showed a similar shift in the preferred size of prey as standard length increased from 30 to 40 mm. Fourteen butter sole (17-35 mm SL) caught on 29 May 1979 fed predominantly on small food items, while the gut contents of four larger fish (49-60 mm SL) caught 1 d later were composed of amphipods, cumaceans, and decapods (Table 1). A similar distinction was found in fish collected on 19 July 1979. Neither *C. stigmaeus* nor *Psettichthys melanostictus* altered the taxonomic composition of their diet within the size ranges of fish we examined, although, as with English and butter soles, larger fish ate larger prey.

The guts of all four species were generally <25% full in the morning before 0900 h. Stomach fullness gradually increased during the late morning and afternoon. The correlation between

TABLE 2.—Percent similarity of prey consumed by English sole, *Parophrys vetulus*; butter sole, *Isopsetta isolepis*; speckled sanddab, *Citharichthys stigmaeus*; and sand sole, *Psettichthys melanostictus*, based on the average 1979 diets shown in Table 1.

Species	*I. isolepis*	*C. stigmaeus*	*P. melanostictus*
P. vetulus	0.77	0.29	0.01
I. isolepis	—	0.39	0.05
C. stigmaeus	—	—	0.64

TABLE 3.—Mean numerical proportions of dominant prey items in the guts of *Parophrys vetulus* less than and greater than 35 mm SL.

	SL <35 mm	SL >35 mm
Small benthic prey		
Magelona palps	0.28	0.03
Juvenile bivalves	0.29	0.01
Tellinid siphons	0.13	0.01
Harpacticoid copepods	0.16	0.08
Total	0.86	0.13
Large benthic prey		
Amphipods	0.08	0.46
Cumaceans	0.03	0.30
Decapods	0.01	0.04
Polychaetes	0.0	0.06
Total	0.12	0.86

the time of capture (ranging between 0830 and 1800 h) and average gut fullness for English sole was significant; $r = 0.49$, $P = 0.05$. On 22 March 1979 two otter trawl hauls were made, one at 1000 and another at 1800 h. Guts of 10 English sole ranging in size between 19 and 35 mm SL were examined from both trawls. The diets of both groups of fish were the same, but the fish collected at 1800 h had an order of magnitude more food items in their guts than the earlier collection: 90% full, 198±56 SD items, vs. 10% full, 18±17 SD items. *Isopsetta isolepis*, *C. stigmaeus*, and *P. melanostictus* showed similar daily trends.

Sufficient numbers of English sole of the same size were collected on 23 January and 29 May 1979 to compare the similarity of diets within and between replicate trawls. The PSI was used to quantify the proportion of food items found in common for each possible pair of fish collected on a sampling date. Mean similarity values were then obtained by averaging the PSI values for the fish within the same trawl and for fish collected in different trawls. Comparing replicate samples obtained at the same depth (Table 4), the average PSI for fish guts within the same trawl in both January and May, as well as the mean PSI between fish in different trawls in January, were approximately the same, 50%. The similarity between two trawls at the same depth in May, though, is very low (3%). Table 4 (bottom) also shows a comparison of within-trawl and between-trawl similarity, where trawls were collected at different depths (20 m and 30 m). Again the within-trawl affinities are high in both January and May, as is the between-tow similarity in January. The average PSI in May for fish from different depths is low. The increased between-trawl variability in food habits noted on 29 May was a general feature observed in all late spring and early summer replicate collections of *Parophrys vetulus*. For example, on 13 July 1978, trawls were made at 15 m and 20 m. *Magelona* palps numerically comprised 72% of the English sole diet at 15 m but only 19% at 20 m, while juvenile bivalves and harpacticoid copepods combined to form 19% of the prey consumed at 15 m and 63% at 20 m.

TABLE 4.—Average percent similarity of index of *Parophrys vetulus* diets within and between replicate trawls on 23 January and 29 May 1979.

	Replicates at same depth		Replicates at different depths	
	Within trawl	Between trawl	Within trawl	Between trawl
23 January 1979				
20 m	53%	53%		
20 m and 30 m			71%	66%
29 May 1979				
10 m	50%	3%		
20 m and 30 m			65%	12%

The diet of recently settled English sole changed continually among sampling months. Comparing similar-sized fish (17-35 mm SL) caught in 1979 (Fig. 3) reveals that dominant food items on a numerical basis varied from *Magelona* palps (November 1978, January 1979), juvenile bivalves (March 1979), bivalve siphons (April and May 1979), to juvenile bivalves and harpacticoid copepods (July 1979). Examination of samples collected in 1977 and 1978 showed that the sequence of changes noted in 1979 does not repeat each year. *Magelona* palps, which in 1979 were never a dominant item in the diet of *P. vetulus* after January, were numerically the most abundant food on two sampling dates in the summer of 1978. Other between-year differences exist, e.g., 5 September 1978 and 24 September 1979, but it is impossible to determine whether these differences are real or a result of spatial variability in diet combined with insufficient sampling.

The apparent increased equitability of prey items shown in Figure 3 for April and May relative to January and March does not indicate that spring and summer diets of individual fish are more diverse than in winter. Instead, the difference is an artifact of the spatial variability previously noted, being generated by averaging the data for all fish caught in different tows. The average dietary diversity (H') of an individual fish on 23 January 1979 (0.43±0.35 SD, $n = 24$) was not significantly different from that on 29 May 1979 (0.37±0.41 SD, $n = 32$).

The only seasonal data currently available on the abundance of benthic organisms at Moolach Beach are for nematodes and harpacticoid copepods. Nematodes are very abundant ($\bar{x} = 1{,}050 \cdot 10\ cm^{-2}$), but quantitatively, with the exception of one sampling date, are not significant in the diet of the fish species we studied. Harpacticoids are important in the diets of English and butter soles, yet are not abundant at the study site. Their average density for the eight sampling dates between July 1978 and September 1979 was 12.2±4.0 SE $\cdot$ 10 cm^{-2}. Only the larger species found in the 0-1 cm depth increment were present in fish guts. *Halectinosoma* spp. comprised more than 80% of all harpacticoid prey.

Seasonally, *Halectinosoma* ranged in abundance from a mean of 6.8 · 10 cm^{-2} between May and September ($n = 5$) to zero from October to March ($n = 3$). Their period of maximum density coincides with their maximum occurrence in the diet of 17-35 mm SL English sole (Fig. 3).

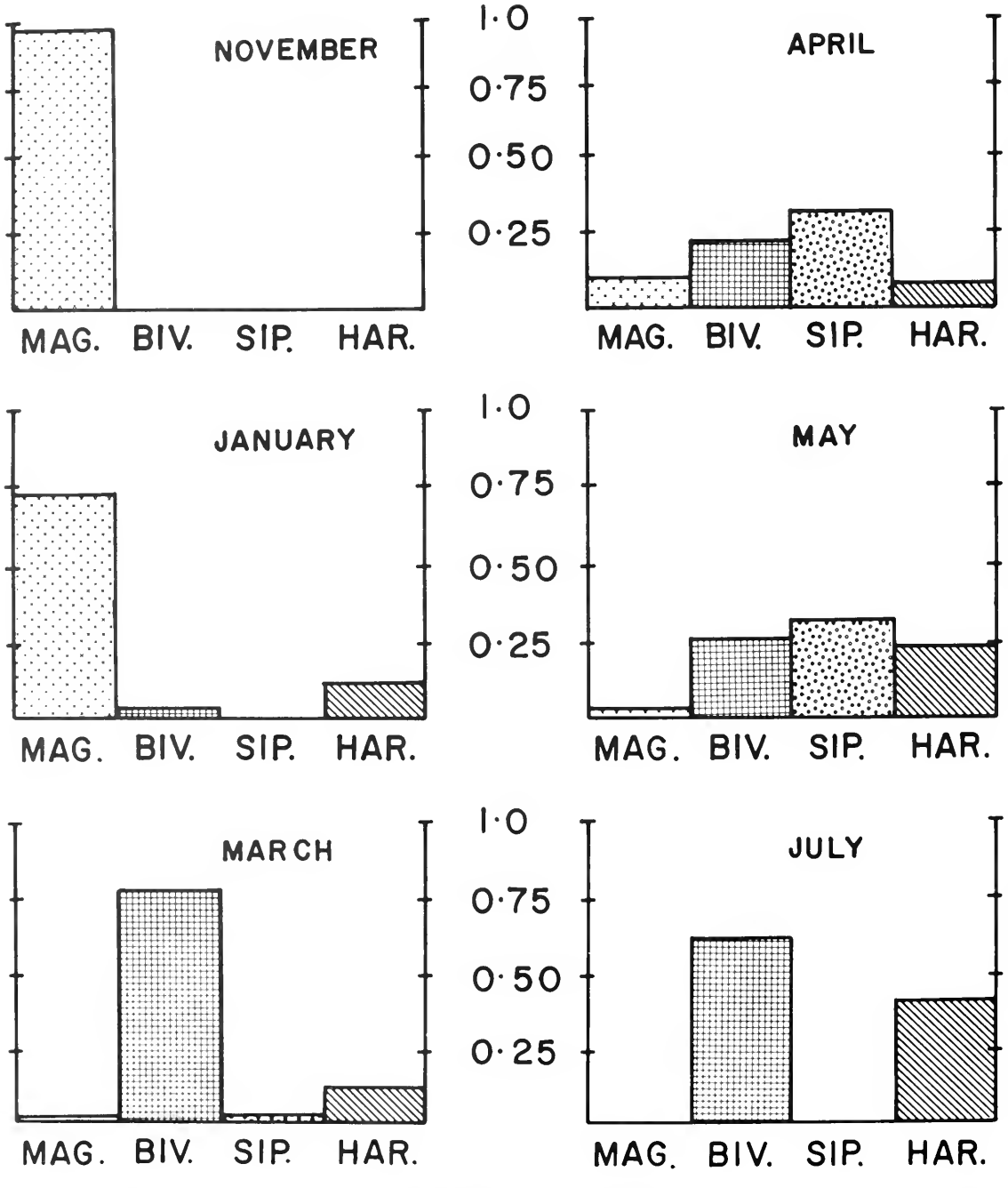

FIGURE 3.—Seasonal change in food habits of *Parophrys vetulus* <35 mm SL between November 1978 and July 1979. Vertical bars indicate average proportion of *Magelona* palps (Mag.), juvenile bivalves (Biv.), clam siphons (Sip.), and harpacticoid copepods (Har.) in the diet.

DISCUSSION

The diet of recently settled English sole is a function of size, location of capture, and season (Tables 1, 3, 4). Both the within-year and between-year differences in diet noted for *P. vetulus* are similar to changes documented for other pleuronectid species (Macer 1967; Edwards and Steele 1968) and are probably related to temporal changes in density of prey organisms. Steele et al. (1970) concluded that variations in predation on *Tellina* siphons and polychaetes by young plaice, *Pleuronectes platessa*, were a result of changes in both the absolute and relative abundances of these prey over time. The observed relationship between seasonal changes in harpacticoid copepod abundance and the utilization of these prey as food by English sole is the only direct evidence we have to support this contention. However, the juvenile bivalves (*Tellina* and *Siliqua*) consumed by *Parophrys vetulus* were all young of the year which are known to have temporally variable recruitment (Jones[5]), suggesting that seasonal availability of this food item is also not constant. Moreover, Oliver et al. (1980) seasonally sampled the nearshore macrobenthos in a region of Monterey Bay, Calif., which was very similar to Moolach Beach in terms of physical environment and fauna present. Their results indicate that the abundance of amphipods and such polychaetes as *Magelona sacculata* vary both within and between years. English sole at Moolach Beach probably alter their diet over time in accordance with similar temporal changes in the density of these larger prey species, but additional benthic data obtained concurrently with fish collections are necessary to substantiate this conclusion.

The marked differences between summer and winter spatial variability in English sole diets (Table 4) are thought to be related to changes in both the abundance and spatial distribution of prey. During the winter, intense storm activity along the Oregon coast produces large waves which continually disturb and mix the sediments of the inner continental shelf (Komar et al. 1972). The meiobenthos has been shown to become randomly distributed during these periods within small areas (1 m^2) and only slightly aggregated on larger scales (Hogue 1982). Small benthic prey fed upon by 0-age English sole would most likely be affected by this vigorous physical mixing in much the same way as the meiofauna. As a result, English sole feeding at either the same depth or different depths may consume similar prey in the winter (Table 4, January) because prey organisms are more evenly distributed within the study area compared to other times of the year. Such a distribution, when coupled with the numerical dominance of one food item, would increase the similarity of food items available for consumption throughout the region. During the late spring and summer the physical disruption of sediment is minimized and the spatial distribution of the meiofauna becomes increasingly aggregated (Hogue 1982). Distinct differences in the species composition and abundance of nematodes and harpacticoids have been found at locations only 250 m apart. During this period there is little similarity in diets of English sole from replicate trawls (Table 4, May). In the spring and summer, *P. vetulus* may be opportunistically exploiting different prey which are densely aggregated in different sectors of the Moolach Beach site.

Seasonal changes in the spatial distribution of prey items may also alter the rate at which prey are consumed. Experiments with fish feeding in aquaria (Ivlev 1961) have shown that an increase in the degree of aggregation of food sources has the same effect on the rate of food consumption as an increase in the concentration of food. Results of Tinbergen et al. (1967) suggest similar relationships between the spatial distribution of prey and predation. Fish commencing their benthic feeding in the late spring and summer at Moolach Beach may benefit energetically from the increased aggregation of benthic organisms during this period relative to that found during the winter.

The consumption of parts of macrobenthic organisms, e.g., *Magelona* palps and tellinid clam siphons, rather than whole individuals by English sole <35 mm in length is probably related to the maximum size of food items capable of being captured and ingested by these fish. We measured the mouth size of 30 mm *P. vetulus* and found that prey greater than about 2 mm in their largest dimension are too large to be consumed by such small fish. Siphons and palps are apparently the only portion of larger prey which are available for ingestion by fish <35 mm SL. As fish grow larger than 35 mm, small food items are neglected in favor of polychaetes, amphipods, and cumaceans which yield far more en-

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ergy per individual item. Two fortuitous consequences of this size-dependent predation may be important. First, the dietary overlap between small juveniles and larger fish is minimized, thus conserving food stocks for recently settled individuals. Second, both siphons and palps are capable of being regenerated. By consuming only parts of benthic organisms, food sources are not destroyed and may be cropped again in later months by other individuals following regeneration. This may be particularly important in the case of English sole because juveniles are continuously recruited to the bottom over a 9-mo period (Krygier and Pearcy footnote 2).

The four pleuronectiform fishes we studied form a trophic continuum, ranging from generalists feeding upon numerous benthic prey (*P. vetulus*) to specialists relying on a few pelagic food items (*Psettichthys melanostictus*). *Isopsetta isolepis* and *C. stigmaeus* are intermediate in their position on the continuum. Few published results exist with which to compare ours. Cailliet et al. (1979) investigated the food habits of *Parophrys vetulus*, *C. stigmaeus*, and *Psettichthys melanostictus* at an ocean station in Monterey Bay. The fish they examined were all larger than the ones for which we have data, but the same basic trends emerge. They found that English sole was a generalist, eating a wide variety of benthic food items; sand sole relied almost totally on mobile crustaceans for food; and speckled sanddab fed on pelagic and epibenthic crustacea and occasional infaunal worms and molluscs. Wakefield (footnote 3) has studied the adult food habits of these three species as well as those of *I. isolepis* collected at the Moolach Beach site. Although the specific food items ingested differ for recently settled juveniles and adults at this site, the basic modes of feeding, e.g., infaunal generalist or pelagic specialist, remained unchanged at Moolach Beach as the youngest juveniles mature to adults.

The greatest similarity among diets is between those of *Parophrys vetulus* and *I. isolepis*. Both of these benthophagous species have similar mouths with small, asymmetrical jaws and small incisor teeth. Both complete metamorphosis and commence benthic feeding at the same size (18-20 mm SL). Qualitatively there is no difference in their diet, although quantitatively butter sole occasionally feed more heavily on mysids. Comparing fish of the same size (17-35 mm SL) on 29 May 1979, *P. vetulus* and *I. isolepis* fed on the same prey items in the same proportions. If food should be limiting for these two species, then in the absence of subsequent shifts in food preference the potential exists for competitive interaction. While observing the feeding behavior of *P. vetulus* in the laboratory, several butter sole were placed in the aquaria along with the English sole. *Isopsetta isolepis* were observed to bite the fins of *P. vetulus* and pursue them around the tank. These were casual observations which were only replicated over a 2-d period. Should this aggressive behavior be substantiated by further work, then interference competition between *P. vetulus* and *I. isolepis* in the Moolach Beach area seems likely. On the whole, however, English and butter soles do not settle at the same time or place. *Parophrys vetulus* has a protracted benthic recruitment period, settling to the bottom between November and July in estuarine and coastal waters <30 m deep (Krygier and Pearcy footnote 2). *Isopsetta isolepis*, on the other hand, has a restricted settling period (May-August) yet occurs over a broader depth range (9-60 m) (Krygier and Pearcy footnote 2). If interspecific interactions were occuring between English and butter soles, it is likely that they would be limited to regions of overlap like Moolach Beach in the summer months.

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PRESSURE SENSITIVITY OF ATLANTIC HERRING, *CLUPEA HARENGUS* L., LARVAE[1]

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ABSTRACT

Larval Atlantic herring, *Clupea harengus harengus* L., are known to change their vertical distribution by day and night, but it is not clear if they can sense their depth by perception of hydrostatic pressure. Two experiments were designed to test whether herring larvae would respond to imposed pressure changes by making appropriate compensatory vertical movements and whether such ability could be related to the development of the bulla system (stage I, bulla absent; stage II, bulla liquid-filled; stage III, bulla gas-filled). In the first experiment, pairs of larvae were exposed to a fixed sequence of pressure changes (ΔP) from ±13 cm H_2O to ±66 cm H_2O. Members of simultaneously tested pairs tended to be influenced by one another when responding to pressure change. The response of stage-I larvae tended to first increase and then decrease over a 20-min test period for a given ΔP. Stage-II and stage-III larvae showed better performances in compensating for imposed pressure changes than did stage I. Larvae exposed to a sudden pressure increase of 5 atm (atmospheres) (5,000 cm H_2O) before the experiment did not perform as well as those not so exposed, but the differences were not statistically significant. A second experiment tested the response of individual larvae to randomized sequences of pressure changes. Stage-III larvae moved most frequently to compensate for the pressure changes, but stage-I and stage-II larvae also responded to changes in pressure. Both experiments show that herring larvae of all three stages compensate for applied pressure changes by moving up when pressure is increased and down when it is decreased, but that they rarely move sufficiently far in the vertical plane to fully compensate.

Larval fish are known to change their vertical distribution diurnally. Although this behavior is probably controlled by changes in light intensity, it is not clear whether hydrostatic pressure perception is important in limiting or controlling the depths reached at different stages of the vertical migration cycle. A few workers (e.g., Qasim et al. 1963) have shown that fish larvae can respond to pressure changes; in particular, Bishai (1961) and Blaxter and Denton (1976) have shown that Atlantic herring, *Clupea harengus harengus* L., larvae are pressure sensitive.

The most likely site for a pressure receptor is a gas-filled structure, such as a swim bladder, which, if compliant, undergoes large changes in volume during vertical movements (10 m change of depth being equivalent to 1 atmospheric pressure). However, clupeoids, together with some other groups such as mormyrids, have gas-filled bulla. In herring the bulla appears to be sensitive to pressure changes (Allen et al. 1976; Denton and Blaxter 1976). In herring the prootic bulla has two parts: one filled with gas, the other with perilymph. The two parts are separated by an elastic membrane. This membrane responds to pressure changes, driving the perilymph in or out of a fenestra, which is situated close to the utriculus of the inner ear. The gas-filled part of the bulla is also connected to the swim bladder by a very narrow gas duct. This connection allows the prootic membrane to adapt to slow changes of pressure. If the pressure increases, the membrane bows in and being elastic tends to return to its resting position. The swim bladder wall is compliant and the pressure differential created along the gas duct causes gas to flow into the bulla from the swim bladder. If the pressure decreases, the membrane bows outward (into the perilymph space) and gas flows from the bulla back to the swim bladder.

In the fully functional system described above the bulla may respond to hydrostatic pressure changes, but because the system adapts in 15-30 s, there will be no perception of absolute pressure. In the very early larval stages of herring (from hatching to 18 mm TL) no bulla is present; the bulla appears at about 18 mm and usually is filled with gas by 26 mm. The swim bladder is not fully formed until 35 mm or more (Blaxter

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and Denton 1976). One would predict that herring larvae up to 18 mm would have little or no pressure sensitivity. As the bulla becomes filled with gas but before the swim bladder develops, we would expect very high sensitivity to absolute pressure (no adaptation being possible) and herring larvae from 26 to 35 mm would be in this category. Larger larvae would retain sensitivity to pressure change, but the development of the adaptation mechanism would prevent its being an absolute sense. One also would predict that herring larvae with gas-filled bullas but no swim bladders would be especially vulnerable to large pressure changes that could cause the membrane to burst. Hoss and Blaxter (1979) have shown that herring larvae do appear to be especially vulnerable to large, rapid pressure changes at about this stage of the life history. Blaxter and Hoss (1979) followed the development of the adaptation mechanism, measured its time constant, and have shown that adaptation usually does not develop until a length of >30 mm.

This paper describes a detailed analysis of pressure sensitivity in herring larvae, using the hypothesis that a larva will swim up to compensate for increasing pressure and down to compensate for decreasing pressure and that this is due in part to the development of the bulla system. In the two experiments to be described, particular attention was paid to measuring changes in sensitivity during the development of the bulla-swim bladder system. In addition, the effect of a large, rapid pressure change on subsequent pressure sensitivity also was investigated in one experiment.

MATERIALS AND GENERAL METHODS

Herring were reared from fertilized eggs, using the techniques of Blaxter (1968). The temperature during development increased from about 7°C near hatching to 12°C, 4 or 5 mo later. The pressure sensitivity experiments were conducted in a constant temperature room at 9°-10°C, using the apparatus of Blaxter and Denton (1976). This apparatus consisted of a Plexiglas[4] cylinder 80 cm high and 7 cm in diameter, the transparent wall being marked on the outside to give 16 equal sections numbered 1-16. The surface was designated 0, the bottom as 17. This allowed an observer to record the position of a larva in the cylinder at any given instant with a number from 0 to 17. The pressure in the cylinder could be changed by a preset amount by opening a two-way tap at the top, which exposed the water surface to atmospheric pressure or to positive or negative pressures in a gas reservoir.

Each larval herring was anesthetized after it was tested and the developmental stage of its bulla (stage I, no bulla; stage II, bulla liquid-filled; stage III, bulla gas-filled) was ascertained. A complication arose that the bulla does not become instantaneously filled with gas and may contain only a few or many bubbles. Pressure sensitivity is more likely to be high if the bulla is full of gas. At least 10 larvae of each developmental stage were used.

EXPERIMENT I

Design

Pairs of larvae of approximately equal length and stage of development were tested simultaneously. After a 2-3 min acclimation period at atmospheric pressure, 10 observations on the position of each fish were made at 15-s intervals. The pressure was then changed and the observations were repeated at the new pressure.

The pressure sequence selected was based upon prior research (Blaxter and Denton 1976) and involved changing the pressure from atmospheric to each of the following pressures four times: ±13, ±39, and ±66 cm H_2O (1 cm H_2O = 0.001 atm), for a total of 480 observations and 47 changes of pressure (Fig. 1). This fixed sequence of increasing pressure differentials was chosen to avoid the potential danger of larvae becoming overstimulated initially at the higher pressures. Earlier evidence (Blaxter and Denton 1976) indicated that larvae moved upwards to compensate for increased pressure and downwards to compensate for decreased pressure, and the extent of vertical movement was correlated with the extent of pressure change (ΔP) applied. Large pressure changes early in the sequence might not only block responses to smaller subsequent pressures but might also cause earlier fatigue. Therefore, pressure changes were not randomized and an experiment commenced regardless of larval distribution in the water column. Approximately half the larvae used in Experiment I were preexposed for 1 min to an abrupt pressure increase

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

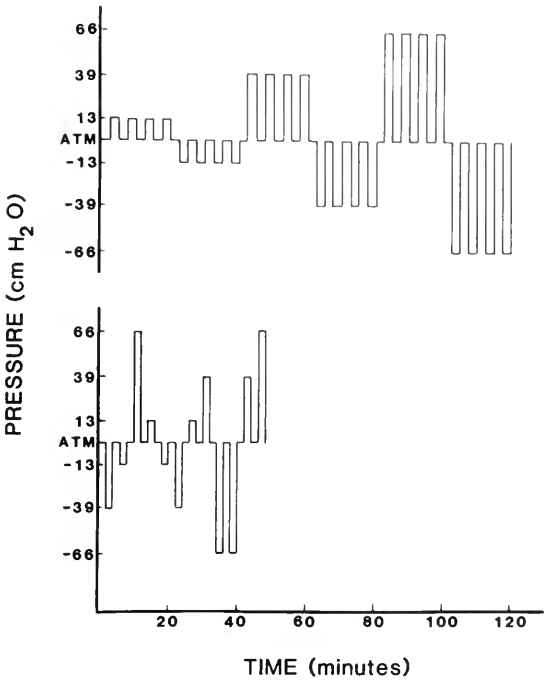

FIGURE 1.—The upper figure depicts the fixed pattern of pressure changes to which pairs of larval herring were exposed in Experiment I. The lower figure shows an example of one of the randomized sequences of pressure changes to which a larval herring was exposed in Experiment II. An independently randomized sequence was drawn for each larval herring tested.

of 5 atm (5,000 cm H_2O) before the onset of the regular pressure series to determine if this abrupt ΔP would impair subsequent pressure sensitivity differently in the different developmental stages. These are referred to as treated larvae, whereas those not preexposed are referred to as control larvae.

Results

Although pairs of larvae selected for simultaneous testing were judged visually to be of equal length, the developmental status of their bulla systems was evaluated only after they were subjected to the pressure tests and was sometimes found to differ (Table 1).

A total of 480 locations within the cylinder were recorded for each herring tested. We averaged 10 locations of a larva during a 2.5-min test at a given pressure to obtain a more concise summary of the response pattern. We then assigned a score to the larva for each 2.5-min series: +, if its average position indicated it had moved in the vertical direction to compensate for the change in pressure; −, if it moved in the opposite direction; and nr, if it showed no net change in its vertical position. We have used these assigned scores in the analyses to follow. Larvae not responding were treated as if they had moved in the noncompensatory direction, so the analyses are conservative. The scoring technique allows one to evaluate the frequency with which a fish, contending with a dynamic pressure regime, moved correctly, i.e., moved in the appropriate vertical direction to compensate for the imposed pressure change.

A separate analysis of variance of the number of compensatory responses was calculated for each treatment group, using only the data for members of homogeneous pairs to determine whether the paired larvae tend to respond together. The intraclass correlation coefficients ranged from 0.91 to 0.92 for the two stage-I groups to 0.20 and 0.32 for the two stage-III groups, respectively (Table 1). Thus for the least, well-developed fish (stage I) the variation among members of a pair was only one-ninth as great as the variation between average values for pairs of fish, i.e., the two members of a pair tended to respond together as a unit. The stage-II control group was an exception to this general pattern. For that group the variation among members of a pair was greater than the variation among pairs, suggesting that the members of a pair tended to move away from one another as pressure within the cylinder was changed.

The lack of independence in the responses of fish tested simultaneously invalidates use of the data for mixed pairs (i.e., pairs of fish of different developmental stages) and requires that we consider pairs of larvae as the experimental unit in testing hypotheses about the average performances. An analysis of variance of data for homo-

TABLE 1.—Numbers of herring larvae, numbers of pairs of larvae of the same developmental stage, and intraclass correlation coefficients for fish tested in Experiment I.

	Control	Preexposed to 5 atm (treated)
Stage I		
Number of individuals	9	8
Number of homogeneous pairs	4	4
Intraclass correlation coefficient	0.92	0.91
Stage II		
Number of individuals	15	11
Number of homogeneous pairs	4	4
Intraclass correlation coefficient	−0.42	0.41
Stage III		
Number of individuals	10	11
Number of homogeneous pairs	2	4
Intraclass correlation coefficient	0.20	0.32

geneous pairs disclosed that stage-I fish moved vertically to compensate for the imposed pressure changes less often than those possessing a more developed bulla system (Table 2). No advantage for fish possessing gas-filled bullas rather than liquid-filled bullas was detected. Although there was a consistent tendency for herring previously exposed to 5 atm to move vertically to compensate less frequently than those not so exposed, this tendency was not statistically significant. The overall intraclass correlation coefficient was 0.67, implying that the average variation among pairs within a treatment group was twice that between members of a pair.

The hypothesis testing reported above ignores the fact that a larval herring could respond in three ways to the 47 changes in pressure; it could move vertically to compensate, it could move vertically in the opposite direction, or it could simply maintain its current position within the cylinder. A plot of the data for pairs of larvae shows that nonresponse to changing pressure was more frequent for stage-I larvae than for the more developed fish (Fig. 2). Two pairs of larvae in particular, one for the stage-I control group and one from the stage-I treated group, are clearly outliers, showing no response during 49% and 86% of the trials, respectively. If these two pairs are dropped from the analysis, then the differences reported above are no longer significant and the means are 27.7 and 25.2, respectively (instead of 23.8 and 19.8) and are close to those for the corresponding stage-II groups (Table 2).

A plot of moving averages of the percentage of compensatory responses against the sequential series of pressure changes reveals that the stage-I herring exhibited a rather consistent pattern of response over the 20 min test period for a given ΔP, especially for the larger ΔP's (Fig. 3). Performance improved at the onset of a new increment or decrement of pressure and then fell off as the test continued, only to improve when the next increment or decrement was used. The other two developmental stages showed a relatively high initial frequency of compensation that rapidly decreased, then subsequently increased until the test of the final pressure change.

TABLE 2.—Analysis of variance of number of compensatory moves of fish during pressure sensitivity tests, and table of means: I = bulla absent, II = bulla liquid filled, III = bulla gas filled.

Source	df	Mean square	F
Preexposure	1	45.47	0.49
Developmental stage	2	314.26	3.40
II versus III	1	88.05	0.95
I versus II and III	1	540.47	5.85*
Interaction	2	28.48	0.31
Experimental error	16	92.44	5.08**
Sampling error	22	18.20	

Intraclass correlation coefficient = 0.67

Average number of compensatory moves per fish:

	Control	Preexposed to 5 atm
Stage I	23.8 (51%)	19.8 (42%)
Stage II	28.9 (61%)	26.1 (56%)
Stage III	32.2 (68%)	30.5 (65%)

*$P<0.05$; **$P<0.001$.

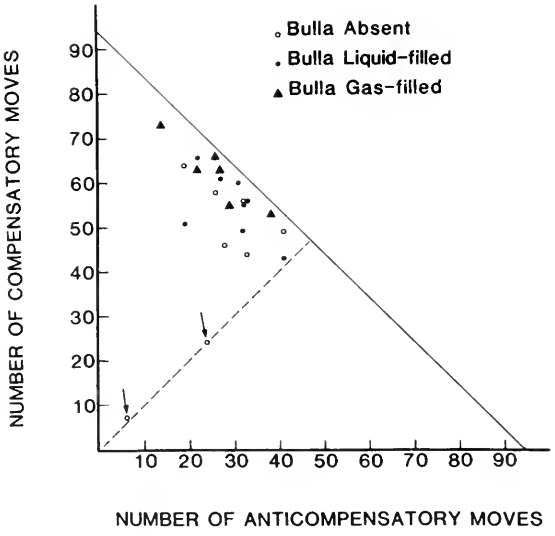

FIGURE 2.—Total numbers of compensatory vertical movements of a pair of herring plotted against the corresponding number of anticompensatory movements for that pair. The dashed line indicates the evenly divided response expected under the null hypothesis. Nonresponse is indicated by the vertical (or horizontal) distance from the hypotenuse. Control and preexposed pairs are not plotted separately. Arrows indicate two outliers.

Discussion

The results in Figures 2 and 3 clearly show that some larvae are responsive to pressure. However, the relatively small sample size, the correlation in the behavior between members of a pair simultaneously tested, and the relatively high variation in response among experimental units within a given treatment group reduced our ability to distinguish differences in the response to changes in pressure of herring of different developmental stages. Additional problems in interpreting the first experiment arose from the evidence that tests of a given pressure

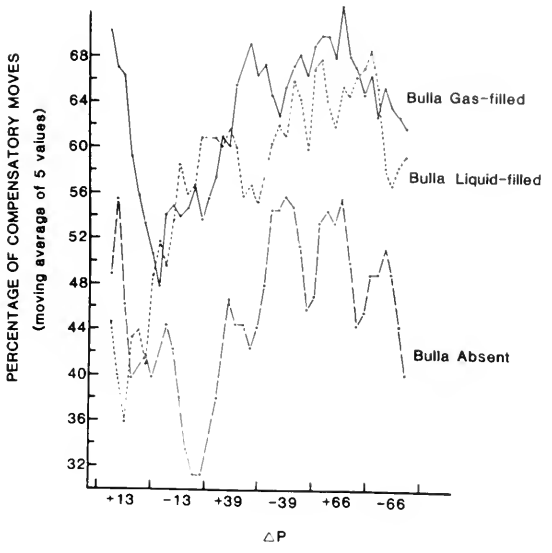

FIGURE 3.—Moving averages of the percentage of correct vertical movements for the three developmental stages of herring in the first experiment. Data for control and preexposed herring are not plotted separately.

change were too long and that the test series as a whole was too protracted as well. The fixed nature of the pressure series, while reducing the chance that larvae would be overstimulated if initially exposed to higher pressure changes, confounded possible differences in response to different pressure changes with habituation to the stimulus or possible learning effects. A second series of experiments was designed therefore to reduce or eliminate some of these problems.

EXPERIMENT II

Design

The major features of the second design were:

1) a single factor, developmental stage of the bulla system; 2) all herring tested individually; 3) an independently randomized test sequence for each fish; 4) each pressure change tested twice; 5) shorter duration of the test series (Fig. 1b) (the larvae were subjected to 23 changes of pressure rather than 47 as in the first experiment); and 6) experiments started when herring were at the center of the test column. Eleven herring of each developmental stage were tested.

TABLE 3.—Analysis of variance of the number of compensatory responses of herring in the second experiment and table of means: I = bulla absent, II = bulla liquid filled, III = bulla gas filled.

Source	df	Mean square	F
Developmental stage	2	62.9394	5.86**
I versus II	1	0.4091	0.030
I and II versus III	1	125.4697	11.68**
Experimental error	30	10.7394	

Average number of compensatory responses per fish:

Stage I	14.18 (62%)
Stage II	13.91 (60%)
Stage III	18.18 (79%)

**$P<0.01$.

Results

As in the first experiment, average positions within the test cylinder were calculated for each pressure change. Vertical movements, as indicated by successive differences in these averages, were then scored as compensatory, anticompensatory, or no response. Analysis of variance of the number of scores indicated that herring with gas-filled bullas compensated more frequently than herring having either liquid-filled bullas or no bullas at all (Table 3; Fig. 4). The stage-III herring on the average moved vertically to compensate 79% of the time compared with 60% and 62% for stage-II and stage-I herring, respectively. However, in Figure 4 we show that even several stage-I larvae achieved relatively high scores, suggesting that a different test of the hypothesis might be based upon classifying larvae into two

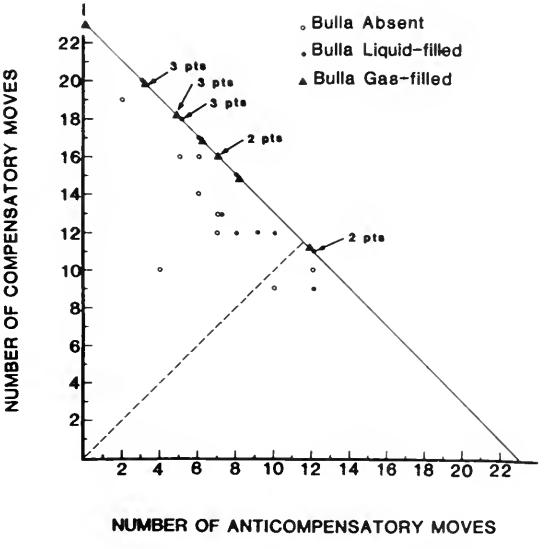

FIGURE 4.—Total numbers of compensatory vertical movements by individual herring in Experiment II plotted against the number of anticompensatory moves. (See legend for Fig. 2.)

categories: 1) those that made more compensatory movements than one would expect by chance, and 2) those that did not.

In Experiment II, each herring was exposed to a random sequence of 23 changes in pressure. If we regard nonresponse as noncompensatory, then the binomial distribution provides a basis for classifying the larvae into two groups, those that moved in the compensatory direction more frequently than one would expect by chance, and those that did not. Under the null hypothesis the probability that a herring would make 16 or more compensatory shifts in vertical position is <0.05. Using this criterion, we classified 5 of the stage-I larvae, 4 of the stage-II larvae, and 10 of the stage-III larvae as having made more compensatory vertical movements than one would expect by chance. A chi-square test showed that the stage-III larvae more frequently compensated for the imposed pressure change than the two earlier stages (chi-square = 7.69, df = 2, $P<0.03$). This implies that the bulla system contributes to the larval herring's hydrostatic pressure perception only after it contains gas.

Because the average position of a larval herring was determined for each pressure level, we could calculate the average vertical distance it moved for each change in pressure. The average distances moved for the 19 successful fish were regressed against the corresponding change in pressure (Fig. 5). The lines for stage-I and stage-II larvae nearly coincide and their slopes are about half that of the regression for stage-III herring. The greatest departure from these lines, fitted through the origin, is for the stage-III herring at the −66 cm H_2O ΔP. They failed to move downward in the column as much as their performance at other pressure changes would predict. We note that even the stage-III herring moved only about 17% of the distance required to compensate fully for an imposed pressure change.

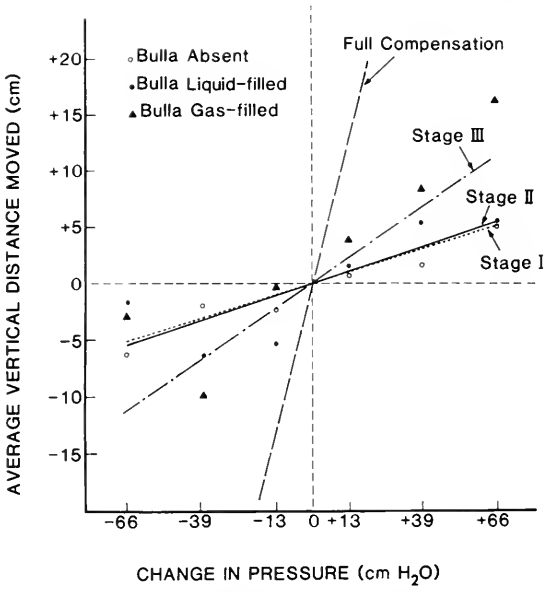

FIGURE 5.—Average vertical distances moved by herring larvae to compensate for changes in pressure.

Discussion

The average proportion of tests in which a larval herring moved vertically to compensate was higher in the second experiment than in the first. This was probably due to the shorter duration of the trials and the test series which should have reduced any effects of habituation or fatigue. However, the random nature of the pressure changes in the second experiment may also have contributed to the enhancement of the response.

Both of the experimental designs employed in this investigation yielded information. The first design revealed that when two herring are tested simultaneously, the response of each is influenced by the presence of the other. It also revealed that the response of a herring to a repeated pressure change tends to increase and then decrease over a 20-min period. The second design provided a more satisfactory test of the null hypothesis that a herring's response to pressure change is independent of the developmental stage of the bulla system and also confirmed an implication from the first experiment: namely, that even before the full development of the bulla system, herring are capable of detecting changes in pressure of the magnitude used in this investigation. Finally, the second experiment demonstrated that herring possessing a gas-filled bulla system will exhibit a markedly improved performance when compared with less mature larvae.

In very few instances did the larvae move a sufficient vertical distance to fully compensate for the imposed pressure change—a similar finding to that of Blaxter and Denton (1976). Even the stage-III larvae, on the average, only moved 17% of the distance to compensate fully. This is partly a statistical artifact of the manner in which we measured a larva's response. We re-

corded its position at 15-s intervals over the 2.5-min period of a given ΔP and then averaged those 10 values. Thus, unless a larva either overcompensated or fully compensated during the first 15 s, its average position during the 2.5-min test would necessarily not be at the level of compensation.

The vertical and horizontal limits of the apparatus also probably impeded vertical progress of larvae in some instances, because the position of the larva within the apparatus at the initiation of a change in pressure determined the potential vertical distance the larva could move to compensate; this would be most important as a source of bias at the larger ΔP's.

Still another possible explanation for the incomplete nature of the compensation may lie in the artificiality of the experiment. Fish are not normally subjected to abrupt hydrostatic pressure changes as they swim with a vertical component. It is difficult to design an experiment to show a hydrostatic pressure sense in a free swimming vertically moving fish larva. Gibson[5] has shown, however, that the activity of juvenile plaice (which lack a swim bladder) varies regularly during sinusoidal changes of hydrostatic pressure of amplitudes of about 50 cm H_2O repeated over a 4-h period, thus demonstrating sensitivity to slow changes of pressure in a fish without a swim bladder.

The site of pressure sensitivity in the herring larvae has not been identified, but it seems to be related to the bulla because sensitivity is enhanced when the bulla is full of gas. It is possible that abrupt changes of pressure applied to the top of a column of water might generate particle displacements in the water that could be perceived by neuromast organs. We do not believe this is a likely explanation of the observed pressure sensitivity in stage-I and stage-II larvae, however, because in some experiments the pressure change was applied over about 5 s, which reduced any resonant effects in the apparatus, but was equally successful in causing correct responses.

Because the swim bladder serves as a gas reservoir for the bulla, the bulla cannot provide perception of absolute pressure for a juvenile or an adult herring. However, in the larva the development of the gas-filled bulla precedes that of the swim bladder and therefore the bulla may temporarily serve as a depth indicator (Blaxter et al. 1981), permitting a larva to limit the maximum depth reached during vertical movements initiated by changes in light intensity. Having a mechanism to limit the maximum depth of vertical migration may enable a larva to maintain its position in the water column. This could be of adaptive value similar to that described for anchovy by Hunter and Sanchez (1976), in that it may serve to keep larvae together and facilitate the development of schooling. A depth indicator might also serve as an energy-saving mechanism if it enables a larva to maintain its position in that portion of the water column where food is most abundant.

In conclusion, we have found that herring larvae display pressure sensitivity both before and after the bulla system has developed, although it is enhanced in larvae with a gas-filled bulla. The threshold of sensitivity was not determined but lies below 13 cm H_2O (1 cm Hg). For a herring larva near the sea surface this observation implies that pressure sensitivity is $<1.3\%$ of the ambient pressure. Prior treatment of larvae to 5 atm pressure did not significantly impair sensitivity.

[5]R. N. Gibson, Principal Scientific Officer, Dunstaffnage Marine Research Laboratory, P.O. Box No. 3, Oban, PA34 4AD, Argyll, Scotland, pers. commun. March 1979.

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FEEDING ECOLOGY OF SOME FISHES OF THE ANTARCTIC PENINSULA[1]

ROBERT A. DANIELS[2]

ABSTRACT

Feeding ecology of 19 species of Antarctic fishes is examined. All species are carnivorous; the most important prey are amphipods, polychaetes, and isopods. Seven of the species examined (*Notothenia neglecta, N. gibberifrons, N. nudifrons, N. larseni, N. kempi, Trematomus scotti*, and *T. bernacchii*) are feeding generalists with diets varying with size of fish, season, and locality of capture. Seven other species (*Trematomus newnesi, Pleuragramma antarcticum, Cryothenia peninsulae, Artedidraco skottsbergi, Harpagifer bispinis, Prionodraco evansii*, and *Parachaenichthys charcoti*) are specialists, feeding predominantly upon prey either from a single taxon or from very few taxa. Five species (*Notothenia rossii, Trematomus eulepidotus, Cryodraco antarcticus, Pagetopsis macropterus*, and *Chaenocephalus aceratus*) were not well represented in the samples, but a qualitative description of their diet is included. The fishes studied consume a wide variety of food types and use several feeding behaviors. Based on field and laboratory observations, most species are ambush predators. However some species use an indiscriminant slurp method, grazing, or a search and capture form of feeding. Some species switch feeding behaviors seasonally or with locality. Diet similarity is high only in morphologically similar species. Where a high degree of diet similarity occurs, overlap in distribution tends to be low. Although most species are high-level carnivores and at least some occur sympatrically, direct competition for food among the species does not appear to exist. This partitioning of food resources adds to the complexity of the structure of Antarctic communities. The position of these fishes in the Antarctic trophic structure should be further examined and considered before extensive exploitation is begun.

Feeding ecology in Antarctic fishes has, until recently, attracted little attention. Richardson (1975) described the diets of four species of fish found along the Antarctic Peninsula and discussed diet overlap. In a thorough study, Targett (1981) examined the trophic structure of five demersal fish communities off Antarctic and sub-Antarctic islands. Permitin and Tarverdiyeva (1972, 1978) examined degree of diet similarity among 10 fishes from the sub-Antarctic island, South Georgia, and in nototheniids and channichthyids collected from the South Orkney Islands, an archipelago north of the Antarctic Peninsula. Moreno and Osorio (1977) examined diet changes with depth in one species, and Wyanski and Targett (1981) reported on diets of nine harpagiferids. Others (Arnaud and Hureau 1966; Holloway 1969; Arnaud 1970; Hureau 1970; Everson 1970; Permitin 1970; Meier 1971; Yukov 1971; DeWitt and Hopkins 1977; Moreno and Zamorano 1980; Duarte and Moreno 1981) described one component of the diet of various fishes, the diet of one species or qualitative descriptions of stomach contents. This study examines several aspects of feeding ecology of Antarctic fishes, including seasonal, spatial, and size-related changes. With increasing interest in the exploitation of Antarctic resources (Lyubimova et al. 1973), the need to understand the feeding ecology of these fishes and their position in Antarctic communities has become important.

STUDY AREA

The Antarctic Peninsula reaches north from the continent to lat. 63°18′S, long. 55°02′W. Its west coast is flanked by numerous islands which create many bays, inlets, straits, and small coves. Weather conditions and longevity and distribution of fast and brash ice vary along the peninsula seasonally, yearly, and with area. Water temperatures at Palmer Station (lat. 64°46′S, long. 64°04′W) fluctuate approximately 2°C from 0°C; salinities range from 32.2‰ to 33.5‰ except immediate to shore and in surface waters during the spring thaw; dissolved oxygen remains near saturation at 6-10 cc/l; pH ranges from 7.9 to 8.5 (Krebs 1974; Showers et al. 1977). Primary productivity varies greatly along the peninsula (Krebs 1974) and in the Antarctic in

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general (El-Sayed 1968) through the year. The composition of the sea bed varies among mud, rubble, and bedrock. Mud bottoms, consisting of glacial flour and diatomaceous oozes, are most common and are found in most straits, bays, and large inlets. Rubble bottoms, composed of heterogeneous mixtures of gravel, cobbles, and boulders, are generally found in small, protected, nearshore coves. Rock cliffs are common along coastal areas and on many submerged mounts. Each bottom type supports a distinctive fauna (Lowry 1969; DeLaca 1976; Kauffman 1977; Daniels and Lipps 1982). Approximately 40 species of fish are found off the Antarctic Peninsula (DeWitt 1971). Table 1 provides a brief description of the species included in this study.

METHODS

Fish used in this study were collected at 11 sites from Terra Firma Islands, Margurite Bay (lat. 68°42′S, long. 67°32′W) to Low Island (lat. 63°25′S, long. 62°10′W) using otter and Isaacs-Kidd trawls, long lines, barrel nets, mud grabs, and hand nets used by scuba divers between 27 January and 28 December 1975 (Fig. 1). Samples were taken at most sites in February or March; a second collection was taken in December at four sites. In areas adjacent to Palmer Station, fish were collected at monthly intervals from January to December.

Fish were preserved immediately in 4% buffered formaldehyde solution; preservative was injected into the stomach cavities of larger specimens. Most species did not regurgitate stomach contents when placed in preservative. However, most channichthyids everted their stomachs when caught; therefore, these species are not included in the analysis and only a qualitative description of their diets is presented. A total of 1,609 stomachs of 19 species were examined. Each of the major Antarctic families is represented: 12 nototheniids, 2 harpagiferids, 2 bathydraconids, and 3 channichthyids. Specimens were later measured (standard length

TABLE 1.—Distribution and morphometric data of fishes collected off the Antarctic Peninsula, 1975. Information on ranges from Norman (1940) and DeWitt (1971).

Species	Distribution	Probable habitat	Relative abundance in samples	Basic body shape	Adult size range (SL mm)	Position of mouth
Nototheniidae						
Notothenia neglecta	circumpolar	rubble-algae	common	bullheadlike	200-300	terminal
Notothenia gibberifrons	Antarctic Pen. South Georgia Scotia Ridge	mud	abundant	bullheadlike	200-300	subterminal
Notothenia nudifrons	Antarctic Pen. South Georgia Scotia Ridge	rocky cliff, mud	abundant	fusiform	100-150	terminal
Notothenia larseni	Antarctic Pen. South Georgia Scotia Ridge	column, bentho-pelagic	abundant	fusiform	100-150	terminal
Notothenia rossii	circumpolar	rubble-algae	rare	bullheadlike	200-300	terminal
Notothenia kempi	Antarctic Pen.	pelagic, bentho-pelagic	rare	fusiform	150-300	slightly supraterminal
Trematomus scotti	circumpolar	pelagic, bentho-pelagic	abundant	fusiform	100-150	terminal
Trematomus newnesi	circumpolar	pelagic, bentho-pelagic	common	fusiform	150-200	supraterminal
Trematomus bernacchii	circumpolar	rubble-algae	common	bullheadlike	150-250	terminal
Trematomus eulepidotus	circumpolar	rubble-mud	rare	fusiform	150-250	supraterminal
Pleuragramma antarcticum	circumpolar	pelagic	common	fusiform	100-150	supraterminal
Cryothenia peninsulae	Antarctic Pen.	pelagic	rare	fusiform	100-150	slightly supraterminal
Harpagiferidae						
Artedidraco skottsbergi	circumpolar	mud	rare	bullheadlike	75-100	terminal
Harpagifer bispinis	Antarctic Pen. South Georgia Falkland Is.	rubble-algae	common	bullheadlike	75-100	terminal
Bathydraconidae						
Prionodraco evansii	circumpolar	mud	rare	wedgelike	100-125	terminal
Parachaenichthys charcoti	Antarctic Pen. Scotia Ridge	rubble-algae	rare	wedgelike	200-250	terminal
Channichthyidae						
Cryodraco antarcticus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Pagetopsis macropterus	circumpolar	pelagic	rare	wedgelike	100-150	terminal
Chaenocephalus aceratus	Antarctic Pen. South Georgia Scotia Ridge	mud	rare	wedgelike	200-300	terminal

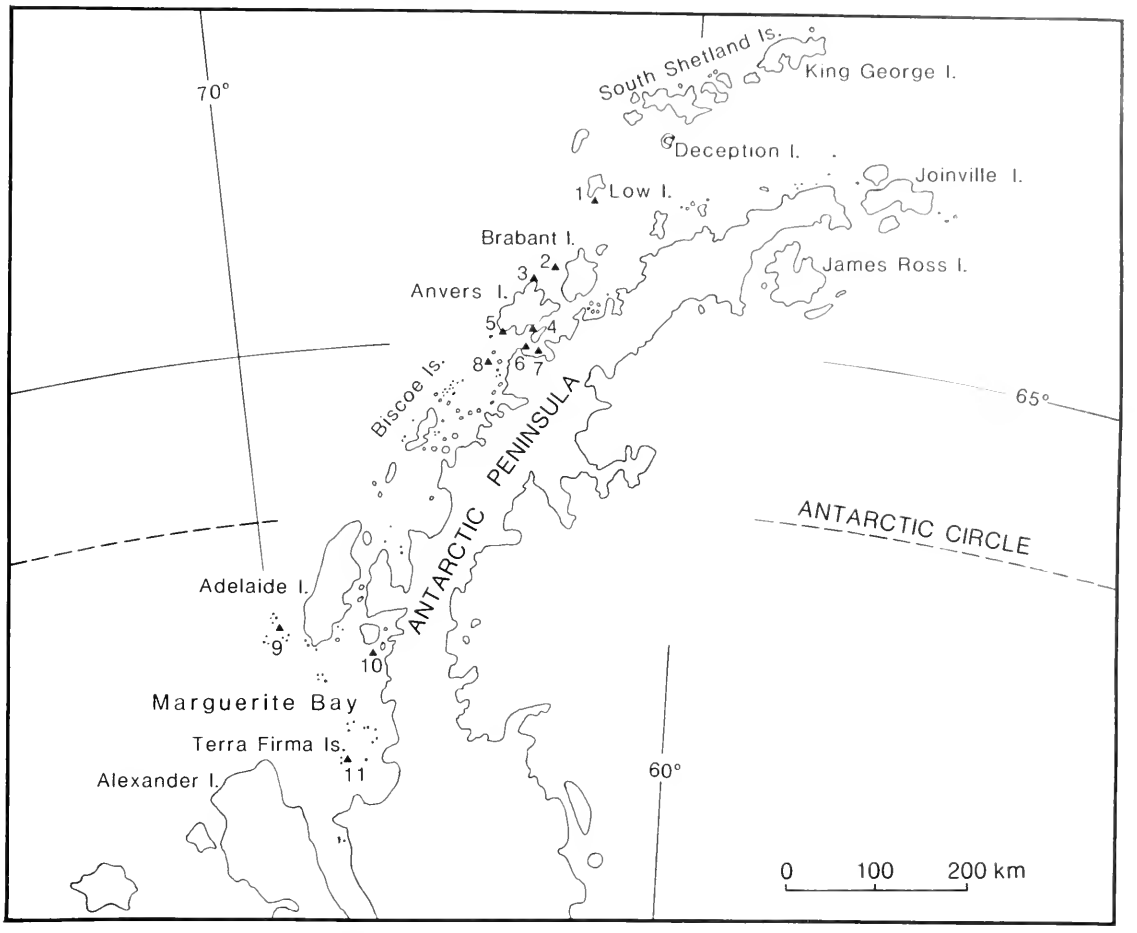


FIGURE 1.—Antarctic Peninsula showing sites where major collections of fish were made, 1975: Low Island (1), Dallmann Bay (2), The Sound, Melchior Islands (3), Port Lockroy (4), Arthur Harbor, site of Palmer Station (5), Peltier Channel (6), Paradise Harbor (7), Argentine Islands (8), Adelaide Island (9), Square Bay (10), and Terra Firma Islands (11).

(SL)), weighed, and dissected. Stomachs were removed, opened, and all contents flushed onto petri dishes. Prey items were sorted, counted, and assigned a point volume (Hynes 1950). One point is approximately equivalent to an isopod *Munna* sp. with an approximate volume of 0.25 ml and approximate dimensions of $15 \times 5 \times 3$ mm; one point was also approximately equivalent to 2 mg dry weight. To test the accuracy of the estimated volumes, the contents of 60 stomachs of *Harpagifer bispinis* were assigned a point volume, volume was measured by displacement, and the contents were dried and weighed. There was little difference between the three measurements (Friedman's Test, $0.2<P<0.3$) (Langley 1970). Individual pieces of algae were not counted and were excluded from all calculations involving number of prey items consumed.

The feeding and foraging behavior of eight species were observed in tanks at Palmer Station and on 140 scuba dives. Twenty-two dives were specifically planned to observe feeding and foraging behavior. In the laboratory, observations were made on recently collected fishes which were introduced into a small cage in a tank where several species of invertebrates were established. The tanks had a gravel substrate, larger rocks, and algae. Invertebrates included in the tanks were scaleworms (*Harmothoe spinosa*), amphipods (*Bovallia gigantea, Eurymera monticulosa*), isopods (*Serolis polita, Munna* sp., *Cymodocea antarctica*), molluscs (*Patinigera polaris, Margarella antarctica, Trophon* sp., *Neobuccinum eatoni*), and echinoderms (*Stere-*

chinus neumayeri, Odontaster validus). After a suitable acclimation period (24-48 h), the fish or fishes were released and allowed to feed. Observations were made from above and provided information on feeding method. Foraging strategy is inferred from the feeding method, morphology, and diet of the fish and microhabitat in which it was captured or observed.

Percentage frequency of occurrence of each prey taxon and percentage composition of diet by number and point volume were calculated for each species. Hoffman (1978) suggested a method for determining an adequate sample size in feeding studies. Using this method, three samples containing 35 individuals of each of four species were examined. No additional information was obtained in sample sizes >9-23 individuals ($\bar{x} = 17$). Where possible, at least 20 individuals were examined. When a sufficient number of specimens was collected, the sample was segregated by size of fish, season, or area of capture. These subsamples were then compared using a χ^2 test for association (Remington and Schork 1970). Fullness indices, measures of feeding intensity (Windell 1971), were calculated for each subsample, and significance was determined by Wilcoxon sum of ranks test (paired samples) or Kruskal-Wallis χ^2 test (3 or more samples) (Langley 1970). Mean prey size was calculated by dividing total volume per taxon by total number of prey items consumed. Percentage diet similarity by number and volume was determined using:

$$S = 100\,(1 - \tfrac{1}{2} \sum_i |p_{xi} - p_{yi}|)$$

where p_{xi} and p_{yi} are the proportions of the diets of species x and y respectively of prey item i (Linton et al. 1981; Abrams 1980; Schoener 1970). Diet diversity was examined by the number of taxa found in the diet of each species (P) and diversity index $H = -\Sigma p_i \ln(p_i)$, where p_i = the proportion of the ith species in the sample (Shannon and Weaver 1949).

RESULTS

Feeding Behaviors

Fishes were observed using variations of four basic behaviors: ambush feeding, bottom slurping, water column feeding, and grazing. Ambush feeding was observed most frequently in the field. *Harpagifer bispinis, Notothenia neglecta, Trematomus bernacchii* usually, and *N. gibberifrons*, on occasion, perched among rocks or partially buried themselves in soft mud and waited for a prey organism to approach. As the prey neared, the fish lunged and then engulfed the item. Treatment of the prey after capture depended upon its relative size and morphology. If possible, the item was swallowed whole. Exceptions to this were scaleworms. In the laboratory, I observed *H. bispinis* capture a scaleworm on 16 occasions, pull it into its mouth, spit it out, immediately pull it into its mouth again, and repeat the process several more times ($\bar{x} = 6$, range = 2-16). This procedure successfully removed all scales from the worm before the fish actually consumed it. This process apparently occurred in the wild since scales are rarely found in *H. bispinis* stomachs although scaleworms are an important part of its diet (below). If the prey item was too large to engulf whole, it was eaten in parts. I observed *N. neglecta* capturing fish one-third to one-half as long as itself on five occasions in laboratory tanks. The predatory *N. neglecta* pulled the prey fish *T. bernacchii* or *N. nudifrons* into its mouth, usually head first, retreated to a protected area, and began to digest that part of the fish in its mouth and stomach. This process took up to 12 h during which time the predator was quiescent. Large prey items taken from the stomachs of *N. neglecta* commonly showed signs of differential digestion, which indicates that this method of feeding occurs in the wild. Fish using ambush feeding tended to be largely carnivorous and preyed upon relatively large, motile organisms. Fishes were observed to take only moving organisms. On many occasions in the laboratory, *H. bispinis* ignored stationary amphipods close to its mouth and readily visible. When the amphipod moved, it was consumed. Often movement consisted only of a twitching antenna.

The slurp feeding method was observed most frequently in *N. gibberifrons* which swam over mud bottoms, sucked up and sifted through large quantities of mud, and consumed the organisms encountered (Daniels and Lipps 1978). Mud and small rocks were also swallowed and passed through the gut. Fish using this method usually fed upon sedentary or slow-moving invertebrates and rarely consumed plant matter. Bacteria adherent to mud may also have been an important part of their diet.

Water column feeding was characteristic of the pelagic *P. antarcticum*, juvenile *T. newnesi*, and, on occasion, demersal forms like *N. neglecta*.

Pleuragramma antarcticum was observed under fast ice in schools of several thousand individuals on three occasions. Individuals darted about and frequently approached the ice-water interface where they appeared to bite at and consume small amphipods (*Nototropis* sp.). Individual juvenile *T. newnesi* also entered the water column under an ice cover or during other periods of low light intensity. These fish generally were found in shallow-water brown algae, *Desmeristia anceps*, beds except when ice was present and light conditions were favorable. They then left the beds individually and occupied the water column where they fed on the undersurface of the ice, or the substrate or in the column. On one occasion, one large *N. neglecta* (400 mm SL) entered the water column and ate several *P. antarcticum* from a school before returning to a rock outcropping. Fishes using this feeding method usually fed upon motile invertebrates, such as eupausiids, pteropods, and amphipods, or other fishes often associated with the pelagic or cryopelagic communities.

Grazing, although never observed, appeared to be an important feeding method in some species, most notably *N. neglecta*, during spring and summer. Individuals were collected with large sheets of macroalgae (e.g., *Phyllogigas grandifolius*, *Iridaea obovata*, or *Desmeristia* spp.), solitary, epiphytic diatoms (*Trigonium acticum*, *Cocconeis imperatrix*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., and *Achnanthes* sp.), and epibenthic diatoms (*Biddulphia anthropomorpha*, *Melosira sol*, *Amphora* sp., *Grammatophora* sp., *Licmophora* sp., *Achnanthes* sp., and *Isthmia* sp.) in their stomachs.

It was inferred from stomach contents that fishes commonly switched from one feeding method and/or foraging area to another with season. *Notothenia neglecta* ambushed prey from rock outcroppings and algae beds through much of the year. During the spring and summer plankton blooms, however, some individuals began to search for food on homogeneous mud bottoms away from any protective rock crannies, as evidenced by large numbers of mud-bottom isopod *Serolis polita* in some stomachs in December. During spring and summer, individual *N. neglecta* cropped macroalgae and harvested diatom mats from mud and gravel bottoms. *Notothenia gibberifrons* used the slurp feeding method to forage in more northern areas but ambushed its prey in southern areas (Daniels and Lipps 1978).

Diets

Diets varied among the 14 species examined so that fishes could be ranked from specialized feeders to feeding generalists (Tables 2, 3, 4). Seven species were generalists (high P and H) and seven species were specialists (low P and H). Generalists consumed a variety of organisms which were phylogenetically and morphologically distinct. Specialists preyed upon organisms with similar morphologies or in the same prey taxon. There appeared to be two types of specialists: in one group, *Cryothenia peninsulae*, *Harpagifer bispinis*, *Artedidraco skottsbergi*, and *Parachaenichthys charcoti*, the diet consisted largely of organisms from one prey taxon; while in the second, *Trematomus newnesi*, *Pleuragramma antarcticum*, and *Prionodraco evansii*, relatively few prey taxa were consumed in approximately equal numbers. Although quantitative data on food availability were not collected, generalists also appeared to be feeding opportunists that ate the most abundant available prey. Individuals in the generalist species also tended to be generalists. Individual *N. neglecta* commonly consumed prey from 5 to 10 taxa (87% of sample) and most of the available prey in the algae beds of Arthur Harbor (Lowry 1969) were found in stomachs of *N. neglecta*. Specialists tended to be more selective. In the rubble bottom community where *H. bispinis* was collected, gastropods, small echinoderms, and errant polychaetes were abundant, yet, except for the scaleworms, which became seasonally important, were rarely found in *H. bispinis* stomachs. Individuals in the specialist species also tended to be specialists; 91% of the *H. bispinis* examined had consumed prey from one or two taxa.

Amphipods were the prey item most fequently taken by fish (Tables 2, 3, 4). However, they were the most important component by volume in only *H. bispinis* and *A. skottsbergi*. Polychaetes were also frequently consumed and were an important part of the diet of *N. nudifrons*, *N. larseni*, *T. scotti*, and *A. skottsbergi* by both number and volume. Isopods, gastropods, and pelecypods also occurred consistently, but were relatively minor components in most diets. Other taxa were important dietary items for only particular species or at particular times of year. Euphausiids, *Euphausia superba* and *E. chrystallorophias*, dominated the diets of *N. larseni*, *T. scotti*, *T. newnesi*, *T. bernacchii*, *Pleuragramma antarcticum*, and *C. peninsulae* by number and volume.

TABLE 2.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (P) and diversity index (H) of fishes of the genus *Notothenia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	N. neglecta			*N. gibberifrons*			*N. nudifrons*			*N. larseni*			*N. kempi*		
	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq (%)	No.	Vol.
Number examined		173			339			164			278			18	
Foraminifera	<1	<1	<1	28	4	<1	<1	<1	<1	4	2	<1	6	2	1
Porifera	<1	<1	<1	4	<1	<1									
Coelenterata	<1	<1	<1	<1	<1	<1				<1	<1	<1			
Ctenophora	2	<1	<1							<1	<1	<1			
Nemertea	10	<1	6	4	<1	1	<1	<1	<1	<1	<1	1			
Nematoda				7	1	<1	3	1	<1						
Bryozoa	1	<1	<1	<1	<1	<1									
Brachiopoda				<1	<1	<1									
Oligochaeta				<1	<1	<1									
Polychaeta, sedentary				65	21	27									
errant	21	<1	2	21	2	9	43	22	45	18	10	12	44	19	31
Mollusca															
Gastropoda	75	10	4	15	2	1	12	4	3	1	<1	<1	11	7	4
Pelecypoda	6	<1	<1	38	8	6	1	<1	<1	<1	<1	<1			
Scaphopoda				3	<1	<1									
Cephalopoda	1	<1	<1	<1	<1	<1				<1	<1	<1			
Arthropoda															
Crustacea															
Amphipoda	94	84	21	54	51	19	66	56	31	39	36	12	22	25	17
Isopoda	15	1	7	7	1	3	23	8	7	5	3	1	28	25	20
Cumacea				9	2	1	1	<1	<1	3	3	<1	17	7	8
Euphausiacea	6	<1	4	6	<1	5	2	<1	1	30	27	54	11	4	9
Ostracoda	3	<1	<1	7	<1	<1	7	2	<1	<1	<1	<1			
Copepoda	15	1	<1	3	<1	<1	1	<1	<1				17	9	4
Pycnogonida	1	<1	<1	2	<1	5	7	2	4	<1	<1	<1			
Echinodermata															
Asteroidea										<1	<1	<1			
Echinoidea	<1	<1	<1	<1	<1	<1	<1	<1	<1						
Holothurioidea	3	<1	<1	1	<1	1									
Crinoidea				1	<1	<1	4	1	5	<1	<1	<1			
Ophiuroidea				9	2	8	<1	<1	<1	1	<1	<1			
Chordata															
Tunicata	<1	<1	<1	2	<1	1	1	<1	<1	3	<1	<1	6	2	1
Pisces	13	<1	28	<1	<1	3				1	2	2			
Egg mass	3	1	1							2	3	7			
Macroalgae	80		21	12		2	3		<1	3		1			
Diatoms	12		3												
Miscellaneous			<1			3			<1			2			5
Taxa (P)		24			28			18			22			9	
Diversity (H)		1.99			2.31			1.53			1.61			1.88	

Fish are a major part of the diet of *N. neglecta* and *Parachaenichthys charcoti* by volume but were unimportant by number.

Changes with Locality

In *N. gibberifrons*, *N. larseni*, *T. scotti*, and *H. bispinis*, the diets of individuals of a similar size group caught at the same time of year but in different localities showed significant differences in the prey taken (Fig. 2) and in the amount of food consumed (Table 5). In each species, approximately the same number of prey taxa were consumed, but only in *H. bispinis* were the taxa identical. The other species consumed not only different amounts from each taxa, but also different types of prey. This change in diet is most dramatic in *N. gibberifrons* (Fig. 2). Individuals from the more northerly Peltier Channel tended to consume sedentary invertebrates such as sedentary annelids, clams, and cumaceans which are often found buried up to several centimeters in the mud. Individuals from the samples of the southern Terra Firma Islands tended to consume motile, rubble-bottom organisms, such as errant polychaetes, amphipods, and fish.

Ontogenetic Changes

Sample sizes were large enough in six species to compare differences in diet with fish size. Within each species, individuals collected from the same locality at the same time but of different size tended to consume prey from the same taxa, but the relative importance of each taxon by volume varied significantly (χ^2, $P<0.02$) (Figs. 3, 4). In all species mean prey size, mean number of prey items consumed, and number of different prey types consumed increased with fish size. Diet diversity showed no size-related change in any species except in *T. bernacchii* (Table 6).

TABLE 3.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (P) and diversity index (H) of fishes of the genera *Trematomus*, *Pleuragramma*, and *Cryothenia* collected off Antarctic Peninsula, 1975. See text for explanation of terms.

	T. scotti			*T. newnesi*			*T. bernacchii*			*P. antarcticum*			*C. peninsulae*		
	Freq (%)	No	Vol	Freq (%)	No.	Vol.	Freq (%)	No.	Vol	Freq. (%)	No	Vol	Freq (%)	No	Vol
Number examined		146			37			76			17			18	
Foraminifera										3	13	2			
Coelenterata	<1	<1	<1												
Nemertea	5	2	2				12	<1	23						
Nematoda	2	<1	<1												
Brachiopoda	<1	<1	1												
Polychaeta, sedentary	23	29	16				4	<1	4				17	6	4
errant	36	14	18	11	6	6	22	2	10	3	2	2	6	1	<1
Mollusca															
Gastropoda	4	2	1	6	3	1	12	1	4						
Pelecypoda	8	3	<1				3	<1	<1						
Arthropoda															
Crustacea															
Amphipoda	29	19	6	47	33	23	72	89	26	7	5	2	6	1	<1
Isopoda	4	3	<1	6	3	1	18	3	12						
Cumacea	7	5	<1							33	53	10			
Euphausiacea	35	13	48	35	53	68	8	4	2	40	24	69	100	92	95
Ostracoda	<1	<1	<1				1	<1	<1						
Copepoda							1	<1	<1						
Pycnogonida	3	1	1				1	<1	<1						
Echinodermata															
Holothurioidea	<1	<1	<1												
Crinoidea	<1	<1	<1												
Ophiuroidea	4	2	1												
Chordata															
Tunicata	1	<1	<1				1	<1	3						
Pisces							1	<1	<1	7	3	3			
Egg mass	<1	1	<1												
Macroalgae	2		1				16		3						
Miscellaneous			2						12						
Taxa (P)		20			5			14			6			4	
Diversity (H)		1 60			0.84			1.97			0 79			0.33	

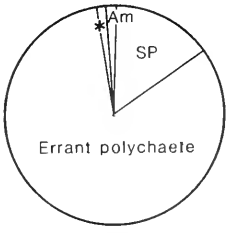
TABLE 4.—Diets by percentage frequency of occurrence, number, and point volume and diet diversity by number of taxa consumed (P) and diversity index (H) of harpagiferids and bathydraconids collected off the Antarctic Peninsula, 1975. See text for explanation of terms.

	Artedidraco scottsbergi			*Harpagifer bispinis*			*Prionodraco evansii*			*Parachaenichthys charcoti*		
	Freq (%)	No.	Vol.	Freq. (%)	No.	Vol.	Freq. (%)	No	Vol.	Freq (%)	No.	Vol.
Number examined		17			237			21			12	
Foraminifera	6	3	<1									
Polychaeta, errant	47	25	47	27	4	16	28	7	19			
Mollusca												
Gastropoda				4	<1	<1						
Pelecypoda				1	<1	<1						
Arthropoda												
Crustacea												
Amphipoda	59	61	46	88	88	79	24	19	29	38	72	8
Isopoda	12	10	5	24	5	4						
Cumacea							38	65	31			
Euphausiacea							19	8	21	50	22	15
Ostracoda				2	<1	<1						
Pisces										25	6	76
Egg mass				6	1	<1						
Macroalgae				8		<1				13		1
Taxa (P)		4			8			4			4	
Diversity (H)		0.88			0.68			1.53			0 72	

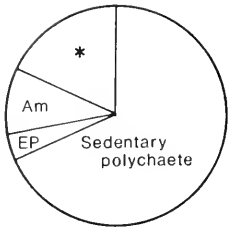
Seasonal Changes

Changes in diet in *N. neglecta* and *H. bispinis* were monitored at monthly intervals in Arthur Harbor through the year. *Notothenia neglecta* showed a significant seasonal diet change ($\chi^2 = 727$, df = 104, $P<0.01$); these fishes switched from being omnivores in the austral spring and summer to a carnivorous diet through autumn and winter. *Notothenia neglecta* also consumed a large variety of organisms, including individuals from several different microhabitats such as isopod *Serolis polita* and nemertean worm *Lineas corrugatus* from mud bottom areas,

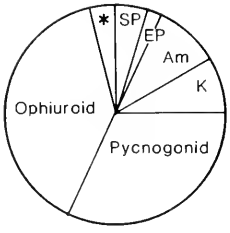
Notothenia gibberifrons



Terra Firma Island n=20

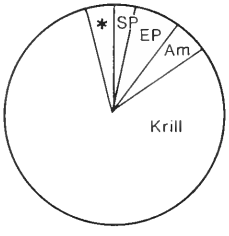


Peltier Channel n=30

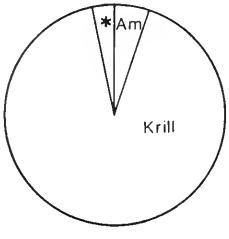


Brabant Island n=24

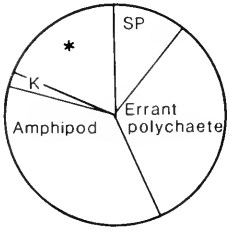
Notothenia larseni



Argentine Island n=30



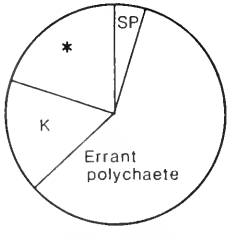
Brabant Island n=29



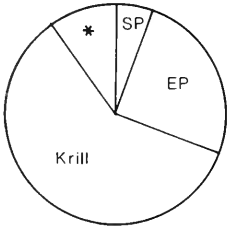
Low Island n=27

KEY
SP - Sedentary polychaete
EP - Errant polychaete
Am - Amphipod
P - Pycnogonid
O - Ophiuroid
K - Krill
I - Isopod
* - Other

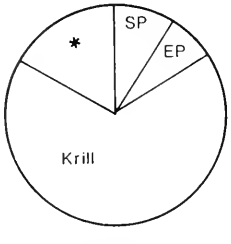
Trematomus scotti



Terra Firma Island n=24

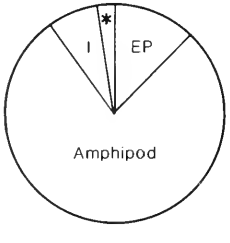


Square Bay n=26



Argentine Island n=33

Harpagifer bispinis



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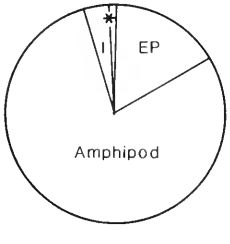
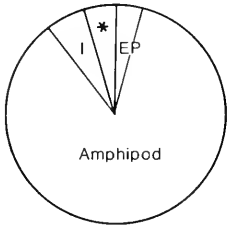
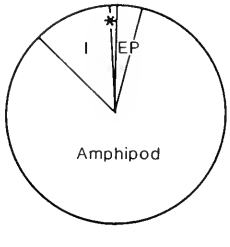


Port Lockroy n=23



Paradise Harbor n=25



Arthur Harbor n=25

FIGURE 2.—Changes in feeding associated with locality of capture in four notothenioid fishes. Fishes used in comparisons are similar in size and were taken during the same season.

TABLE 5.—Changes in diet by locality of capture in fishes of similar size and taken during the same season off the Antarctic Peninsula, 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed; a Kruskal-Willas χ^2 test was used to examine changes in feeding intensity (fullness index).

Species	Area	*n*	SL (mm)	Range (mm)	No. taxa consumed	Volume		Fullness index		
						χ^2	*P*	$\bar{X}$	χ^2	*P*
Notothenia gibberifrons	Peltier Chan.	30	146	106-217	13			6 8		
	Terra Firma Is	20	123	100-146	13			8 2		
	Brabant I	24	134	87-260	12	393.1	<0 01	7.5	8 5	0 05
N larseni	Brabant I	29	120	70-150	4			8 1		
	Low I	27	114	84-152	8			6 6		
	Argentine Is.	30	113	72-162	10	224 6	<0.01	2.4	20 2	<0 01
Trematomus scotti	Terra Firma Is.	24	69	45-90	7			7.0		
	Square Bay	26	98	61-137	9			4 9		
	Argentine Is.	33	99	63-126	15	104 9	<0.01	6.9	15.8	<0 01
Harpagifer bispinis	Argentine Is	20	71	58-80	6			4 4		
	Port Lockroy	23	67	43-82	5			8 4		
	Paradise Harbor	25	68	57-88	5			5 5		
	Arthur Harbor	25	70	51-85	5	42.1	<0.01	8 2	14 1	<0 01

TABLE 6.—Size-related changes in diet in Antarctic fishes, Antarctic Peninsula, 1975. Fish in each species were collected at the same time from the same locality.

Species	Capture	Size group	*n*	SL $\bar{X}$ (mm)	SL range (mm)	Mean no. items/stomach	Mean prey size (vol./item)	No. taxa consumed	Mean *H*
Notothenia neglecta	Arthur Harbor December	I	10	80	71-90	13.8	0.9	7	0 5
		II	8	199	165-231	82.0	4 5	8	0 8
		III	9	292	258-313	37.0	12.8	12	0.6
Notothenia gibberifrons	Peltier Chan. February	I	14	80	49-99	5 8	0 6	10	0.8
		II	20	129	116-148	8.0	1.2	13	0.8
		III	20	193	163-217	10.9	1 8	15	0.9
Notothenia nudifrons	Dalmann Bay December	I	28	50	32-65	4 7	0.2	10	0 7
		II	16	116	93-153	4.3	0.7	11	0 7
Notothenia larseni	Low I. March	I	16	94	82-105	2.7	1 8	4	0 3
		II	19	139	113-157	2.4	3.7	7	0.5
Trematomus scotti	Argentine Is. March	I	18	84	63-99	3.0	1.6	11	0.5
		II	17	121	108-144	2.7	3.3	13	0.8
Trematomus bernacchii	Arthur Harbor June	I	13	69	60-78	15.0	0.5	4	0.1
		II	14	138	107-160	31.4	2.7	8	0.3
		III	14	200	180-233	10.1	8 1	10	0.7

krill and *Pleuragramma antarcticum* from the pelagic and cryopelagic communities, limpet *Patinigera polaris* from rocky cliffs, and a large number of organisms from rubble-bottom areas, the habitat from which this species was most frequently collected. *Harpagifer bispinis* consumed prey from the same taxa through the sampling period, but the importance of each taxon differed ($\chi^2 = 149$, df = 21, $P<0.01$). The significance results from a midwinter peak in abundance of scaleworms. This species consumed organisms from the rubble-bottom community which consisted largely of the amphipods *Borallia gigantea*, *Eurymera monticulosa*, the scaleworm *Harmothoe spinosa*, and the isopods, *Munna* sp. and *Cymodocea antarctica*.

Differences in diet of similar-sized individuals of *Notothenia gibberifrons*, *N. nudifrons*, *N. larseni*, and *T. scotti* collected at the same locality at different times of year were significant in the relative importance of each prey taxon, but tended to show no significance in the amount of food consumed (Table 7). In all four species individuals tended to consume prey from the same number of taxa. Spring samples tended to contain individuals of a smaller size than late summer samples.

Dietary Similarity

Diets were >60% similar in 17 species pairs by number and in 11 species pairs by volume (Table 8). Similarity in diet by number of prey items consumed is greater due to the large number of amphipods taken by most fishes. A high percentage similarity by volume, a value more indicative of the importance of each food type, was obtained for morphologically similar species such as the two harpagiferids, *A. scottsbergi* and *Harpagifer bispinis*, and the pelagic-benthopelagic complex of *N. larseni*, *T. scotti*, *T. newnesi*, *Pleuragramma antarcticum*, and *Cryothenia peninsulae*. Species that were generalists showed 30-60% similarity in diet with other

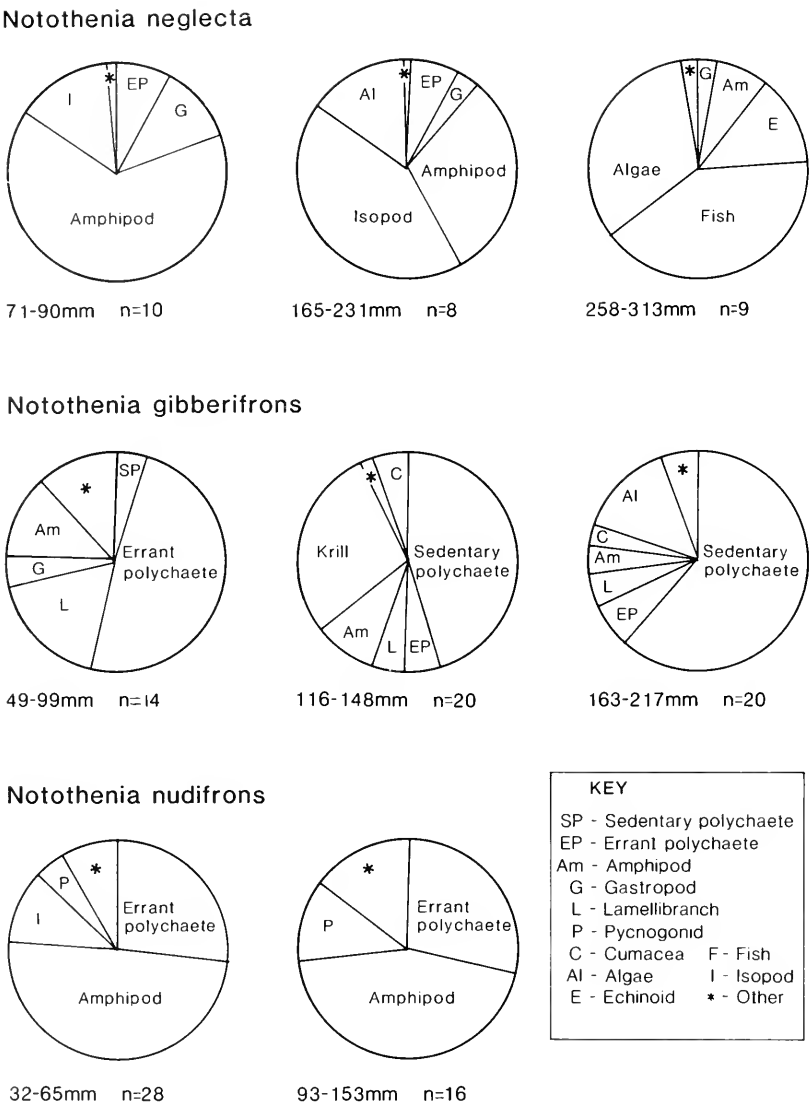


FIGURE 3.—Size-associated changes in feeding in three *Notothenia* spp. collected at the same locality on the same day.

generalists and <30% similarity with the more specialized feeders. Generalists were often collected at sites with other generalists and specialists. The tendency among specialized feeders was one of low percentage similarity in both diet and distribution.

Other Species

Four *N. rossii*, morphologically similar to *N. neglecta*, consumed prey from six taxa. Amphipods were most important by number (81%); krill (31%) and demersal fish (51%) were important by volume. Krill was the most important component by number and volume in the diets of five *T. eulepidotus*, seven *Pagetopsis macropterus*, and eight *Cryodraco antarcticus*. These species consumed prey from relatively few taxa and were exclusively carnivorous. *Trematomus eulepidotus*, morphologically similar to *T. scotti*, in addition to the pelagic krill, also consumed cumaceans which are typically associated with mud bottoms. The channichthyids, *P. macropterus* and *C. antarcticus* also consumed fish, such as

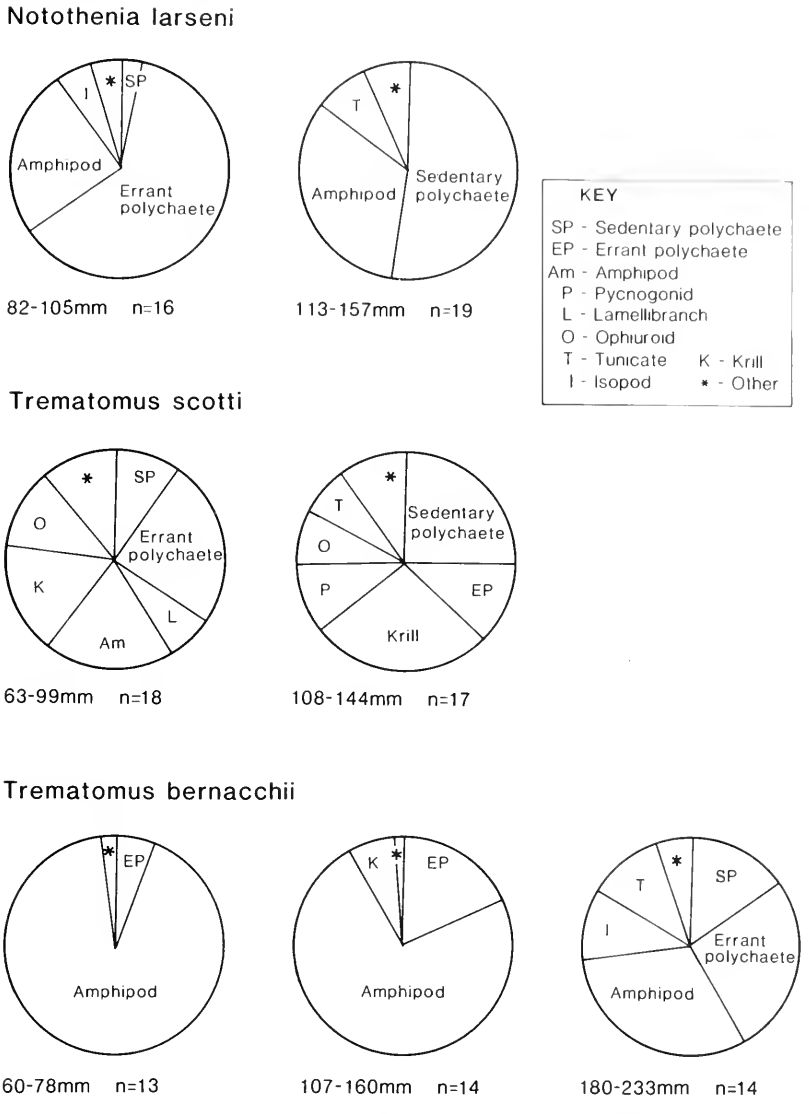


FIGURE 4.—Size-associated changes in feeding in three notothenids collected at the same locality on the same day.

the pelagic *Pleuragramma antarcticum* and the demersal *N. nudifrons*. In one *Pagetopsis macropterus* collected in Margurite Bay, both species of krill found in the area were present. The stomachs of 42 *Chaenocephalus aceratus* were examined and found to be empty.

DISCUSSION

Antarctic fishes show great variety in the type of prey consumed and the behavior used to capture prey. Yet all occupy a similar position in the community, that of a high-level carnivore. Of the 19 species included in this study, all consumed actively moving prey frequently and, with the exception of *N. gibberifrons*, active prey dominated diets. Although the diets of the prey are poorly known, at least some, like *Bovallia gigantea*, *Harmothoe spinosa*, and *Sterechinus neumayeri*, are themselves high-level carnivores (Bone 1972; Brand 1976).

In this study the notothenids show the greatest diversity in both diets and feeding behaviors although a high degree of similarity in diet

TABLE 7.—Seasonal dietary changes in fishes of similar size collected at the same locale off the Antarctic Peninsula, 1975. A χ^2 test for association was used to examine changes in the volume of each taxon consumed. A Wilcoxon sum of ranks test was used to examine changes in feeding intensity.

Species	Area	Date	n	$\overline{SL}$ (mm)	Range (mm)	No. taxa consumed	Volume χ^2	Volume P	Fullness index $\bar{X}$	Fullness index R	Fullness index P
Notothenia gibberifrons	Peltier Chan.	Summer	30	146	106-217	13			6.8		
		Spring	49	138	100-229	13	31.3	<0.01	6.0	1,301	<0.30
	Brabant I.	Summer	25	134	87-260	12			7.5		
		Spring	22	123	106-167	9	114.6	<0.01	2.1	294	<0.01
Notothenia nudifrons	Low I	Summer	20	107	72-140	8			5.6		
		Spring	34	95	47-127	5	80.9	<0.01	5.8	500	<0.74
Notothenia larseni	Low I	Summer	27	114	84-152	8			6.6		
		Spring	25	99	90-142	9	66.7	<0.01	9.5	544	<0.08
	Brabant I.	Summer	29	120	70-150	4			8.1		
		Spring	30	86	60-126	5	27.9	<0.01	2.2	735	<0.04
Trematomus scotti	The Sound	Summer	8	112	88-134	5			6.4		
		Spring	7	101	85-114	5	109.4	<0.01	3.4	47	<0.20

TABLE 8.—Percentage diet similarity by number of prey items consumed (upper triangle) and point volume (lower triangle) in fishes taken off the Antarctic Peninsula, 1975.

	Notothenia neglecta	*Notothenia gibberifrons*	*Notothenia nudifrons*	*Notothenia larseni*	*Notothenia kempi*	*Trematomus scotti*	*Trematomus newnesi*	*Trematomus bernacchii*	*Pleuragramma antarcticum*	*Cryothenia peninsulae*	*Artedidraco skottsbergi*	*Harpagifer bispinis*	*Prionodraco evansii*	*Parachaenichthys charcoti*
N. neglecta	—	58	63	46	33	26	37	89	5	8	61	86	18	71
N. gibberifrons	39	—	61	52	34	51	39	56	13	14	57	55	24	51
N. nudifrons	36	42	—	58	58	44	46	64	10	3	87	66	27	54
N. larseni	28	40	31	—	52	49	67	43	38	29	41	44	37	60
N. kempi	34	40	61	39	—	48	41	32	20	6	56	35	37	29
T. scotti	19	42	30	70	38	—	45	32	27	23	36	27	20	32
T. newnesi	28	31	32	72	34	62	—	43	32	56	42	41	33	55
T. bernacchii	52	37	50	27	42	34	39	—	10	5	66	93	25	77
P. antarcticum	16	11	6	61	22	61	79	18	—	26	10	7	67	30
C. peninsulae	3	11	3	55	10	53	70	12	76	—	2	2	10	23
A. skottsbergi	28	31	67	25	53	25	30	41	5	2	—	70	27	61
H. bispinis	27	33	52	26	38	23	30	41	4	2	66	—	24	72
P. evensii	25	34	49	46	53	46	50	38	35	23	49	44	—	28
P. charcoti	39	16	9	25	17	21	23	12	20	16	9	8	23	—

among similar species is often present. Results from other studies, using fewer species, are similar (Permitin and Tarverdiyeva 1972, 1978; DeWitt and Hopkins 1977; Richardson 1975; Moreno and Osorio 1977; Moreno and Zamorano 1980). This high diversity is attributable to diet changes with size of fish, capture locality, and season.

The harpagiferids, bathydraconids, and channichthyids tend to be more specialized than the nototheniids in both their choice of prey and in the method used to obtain it. Results for *Harpagifer bispinis* can be compared to those of Meier (1971), Richardson (1975), and Wyanski and Targett (1981). In all cases, *H. bispinis* was shown to consume amphipods overwhelmingly. *Artedidraco skottsbergi* consumed polychaetes and amphipods; similar results were reported by Wyanski and Targett (1981). No comparable data are available for the bathydraconids or the channichthyids examined in this study. However, the diets of the five channichthyids examined by Permitin and Tarverdiyeva (1972, 1978) show them to be specialized feeders and, with the exception of *C. aceratus*, planktivorous; my remarks regarding the diets of *P. macropterus* and *Cryodraco antarcticus* corroborate these findings.

The high degree of dietary similarity that I observed among certain fishes and the similarity of diets reported by Permitin and Tarverdiyeva (1972, 1978), and Richardson (1975) do not necessarily imply interspecific competition over food, but do suggest a complex trophic structure not normally associated with communities of high latitudes (Cushing 1975). The benthic fishes studied use a wide variety of mechanisms to assure a constant food supply. For the generalists, these include switching prey types and feeding strategies; the specialists consume prey types which are themselves capable of maintaining stable populations either by switching food by becoming inactive (Dearborn 1967) or by possessing a reproductive biology which in-

cludes high fecundity and long mean generations (Cushing 1975). These stabilization mechanisms provide a constant source of food despite disbalanced primary production. With this constant and relatively abundant food source, competition, which requires a limiting resource (Larkin 1963), does not appear to be common among Antarctic fishes. The fact that high diet similarity is observed argues against competition over a limited food resource as a major factor structuring Antarctic fish associations (Zaret and Rand 1971; Tyler 1972). Where competition may be important, e.g., in the pelagic-benthopelagic fish association, the major prey item is krill, which is abundant. However, this abundance may be temporary and of recent origin. This would obscure the importance of competition in structuring Antarctic associations and points to the need for further study.

The position of fishes in the trophic structure of Antarctic communities is also not well understood. All are carnivorous and many are second or third level carnivores. Whether or not these fishes are themselves consumed in large numbers by the abundant birds and mammals of the Antarctic is poorly known. Some birds consume small species or juveniles of large species (Watson 1975) and several species of seals are reported to consume fish (Dearborn 1965; Stonehouse 1972). However, the species consumed and the relative importance of fish in the diets of these predators remain unknown. It does appear that such predators do not have much of an impact on the large benthic fish populations, since the fishes are extremely slow growing and long lived (Emerson 1970). Thus the impact of heavy and unaccustomed predation (fishing) on this system could be very disruptive. Before extensive exploitation begins, the life history of the organisms to be harvested should be understood.

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THE EARLY LIFE HISTORY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS*

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ABSTRACT

The early life history of Pacific hake, *Merluccius productus*, is described from laboratory and field studies. At ambient temperatures (11°-13°C) egg hatching takes about 100-120 hours; complete absorption of the yolk takes about 150-200 hours. Respiration rates for first feeding larvae at 12°C are 4.8-6.8 μl/mg per hour. Growth rates for at least the first 20 days are slow compared with other larvae in the California Current. First-feeding hake larvae require a daily ingestion of about 0.13 calories.

In this study I present information on the early life history of Pacific hake, *Merluccius productus*, including rates of development, starvation, growth, and metabolism. I have also used samples from Ahlstrom (1959) and others to examine the vertical distribution of eggs and larvae by size class. My objectives in examining these life history processes are to 1) evaluate the hypothesis that the availability of food directly after complete yolk-sac absorption is the critical factor in survival of larval Pacific hake and 2) to determine the relative length of time Pacific hake are in egg and yolk-sac stages and are most vulnerable to invertebrate predators.

The early life history of Pacific hake represents an interesting contrast to other fishes that spawn off the coast of California, including the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*. Compared with these other species the early life history of Pacific hake has been little studied. It is known that hake larvae live below the mixed layer in colder water, and that first-feeding larvae have large mouths, so they can feed on a wide spectrum of food particles (Ciechomski and Weiss 1974; Sumida and Moser 1980). Both the anchovy and mackerel have been subject to intensive investigation as models of the causes of egg and larval mortality. Eggs and larvae of both anchovy and mackerel are found within the warm upper mixed layer (Ahlstrom 1959). Compared with hake larvae, anchovy and mackerel have relatively small mouths at first feeding; thus, the size of ingested food particles is restricted (Hunter 1980). At least for first-feeding anchovy larvae, it has been shown that the availability of food of the proper size and in adequate densities is important to survival (Lasker 1975). The results of the present study, in particular the determination of the food requirements of hake larvae may indicate important differences in the survival strategies of these three fishes.

METHODS

Development and Growth

All laboratory experiments in this study were conducted using eggs collected at Port Susan, Wash. This stock is reproductively isolated from the Pacific hake spawning off the California coast (Utter 1969), but I am assuming that temperature-specific rates of metabolism of larvae hatching from Port Susan eggs are similar to the rates for larvae hatching from eggs spawned in the California Current because 1) egg size is the same, 2) temperature-dependent hatching times are the same (see results this study), and 3) growth to age 2 is the same (Kimura and Millikan 1977).

Eggs were collected with a 500 μm mesh meter net (equipped with a cod end designed to capture live zooplankton) and returned to the laboratory at 5°-10°C. Eggs and larvae were reared in filtered seawater in 1-4 l jars containing 50 ppm each penicillin G potassium and streptomycin sulfate. Egg hatching experiments were done with 3 replicates of 10-20 eggs/l. Percent hatching was checked every 12 h. The eggs used in these experiments were without visible embryos

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and were assumed to be about 12 h old. The time to 50% hatching was determined by interpolation from the linear regression of percent hatching (y) against time (x). Confidence intervals on the 50% hatch time were calculated from the prediction of x from y as:

$$\text{C.L.} = \bar{x} + \frac{b_{yx}(y_i - \bar{y})}{D} \pm H,$$

where $D = b_{yx}^2 - t^2_{(0.05, n-2)} S_b^2$, and

$$H = \frac{t_{(0.05, n-2)}}{D} \sqrt{S_{yx}^2 \left[D\left(1 + \frac{1}{n}\right) + \frac{(y_i - \bar{y})^2}{x^2} \right]}$$

Time to 50% yolk-sac absorption was determined similarly. Survival of yolk-sac larvae appeared to increase substantially under lighting in the cold rooms, which raised temperatures in these experiments to 10.5°C in the 8°C room and to 13.7°C in the 12°C room. The 15°C room was consistently lighted. After hatching at temperature, postyolk-sac larvae were removed, placed in new jars, and observed to determine time to starvation.

Growth was examined by counting daily increments on otoliths. For verification of otolith increments as daily marks, larvae were reared in the laboratory without antibiotics in a 12-h light-dark cycle. Larvae were fed *Artemia salina* nauplii and natural zooplankton strained through a 216 μm mesh net at a concentration of about 1 animal/ml. Field-caught specimens were obtained from several cruises off the California coast in 1977, 1978, and 1979. Both laboratory-reared and field-caught specimens were preserved in 80% ethanol. Larvae were measured (standard length) and otoliths were removed under a dissecting microscope fitted with a polarizing filter. Otoliths were mounted on a glass slide in protex or euparal, and rings on the otoliths were counted at 600-1000× magnification.

Larval dry weights (preserved in 80% ethanol for otolith investigations and in 3% Formalin[2] for respiration investigations) were determined on a Cahn 25 Electrobalance after rinsing the larvae in distilled water and subsequently drying them for 24 h at 60°C. Weight loss due to preservation was determined by comparing weights of subsamples of fresh-frozen larvae and preserved larvae, all hatching from the same cohort of eggs. Shrinkage in length was determined by measuring anaesthetized larvae before preservation and then again after 2-3 wk of preservation in 80% ethanol or 3% Formalin. Shrinkage due to preservation delay and death in a wet cod end during or after a plankton tow was simulated by anaesthetizing and measuring larvae, and then placing them on seawater-wetted paper towels for specific time periods. Larvae were then preserved in Formalin. These preservation effects were tested only on first-feeding larvae.

Growth, egg development, and yolk-sac absorption data were fitted with a Gompertz curve using a least-squares nonlinear curve fitting program (SPSS). The Gompertz growth function was selected because it is a flexible nonlinear function commonly used in studies of larval fish (Zweifel and Lasker 1976).

Metabolic Rates

Respiration rates of larvae were measured using a micro-Winkler technique (Carritt and Carpenter 1966). Experiments were conducted in 30 ml glass stoppered jars, at densities of 2-3 larvae/jar, in dim light for 11-14 h. Larvae in filtered seawater were acclimated to temperatures for 12 h. After the experiments were completed and oxygen fixed, jars were kept for 2-10 d at 8°C in the dark before titrating. Experiments were designed to include 3-5 replicates per temperature; however, when bubbles formed during the experiment (a constant problem at 15°) samples were discarded.

Vertical Distribution

Samples from vertical series of tows taken in 1954 and 1955 were reported by Ahlstrom (1959). I sorted and measured these samples to examine size-related vertical distribution. Pacific hake larvae from an additional three vertical series taken in 1969 were sorted and measured. Since there were no apparent day-night differences, all hauls, day and night, were combined. Nonstandardized data consisting of raw numbers per haul, uncorrected for volume of water filtered, were used since more detailed information did not exist for many hauls. Data on numbers of larvae caught per haul were classified into the depth interval where most of the tow took place.

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

RESULTS

Development Times

Egg hatching time shows a marked response to temperature (Fig. 1). Time for 50% hatching of eggs collected at Port Susan ranges from 3.5 d at 15°C to 4.5 d at 12°C (coastal temperature range at 50 m depth is 11°-14°C) and 6.5 d at 8°C (the approximate temperature at Port Susan). Also shown in Figure 1 are the mean hatching times of eggs collected off California that were reported by Zweifel and Lasker (1976).

The time from hatching to complete absorption of the yolk sac is also temperature dependent (Fig. 2). The time for 50% of the sample larvae to completely utilize their yolks is 9.7 d at 10°C, 6.4 d at 12°C, and 4.2 d at 15°C. I was not able to rear larvae to yolk-sac absorption at 8°C. At 8°C, 8-12 d old larvae still had considerable yolk supplies and no functional mouth. A well-developed mouth normally formed after 4 d at 12°C and after 3 d at 15°C.

Both the mean and the maximum length of time to starvation after complete utilization of the yolk decreased with increasing temperature (Table 1). A nonparametric analysis of variance (Kruskal-Wallis; Conover 1971) indicates that temperature has a significant effect on the time to starvation ($P<0.01$). The variance in the mean time to death was large in these experiments due to death occurring not only from starvation, but from other causes such as being trapped in the surface film. These early nonstarvation deaths were excluded from the analysis.

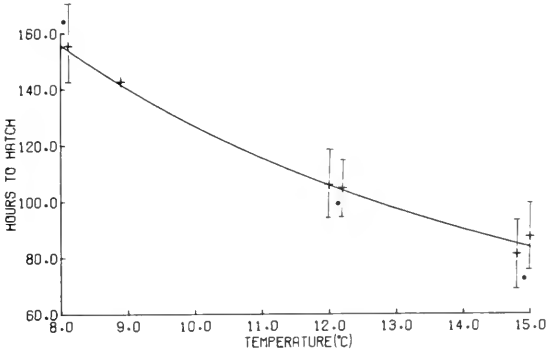

FIGURE 1.—Effect of temperature on time to 50% eggs hatching for Pacific hake, and 95% confidence intervals. Small solid circles are hatching times from Zweifel and Lasker (1976). Data was fitted to a Gompertz curve: $Y = 484.00 * \exp(-2.89 * (1 - \exp(-0.0623 * X)))$.

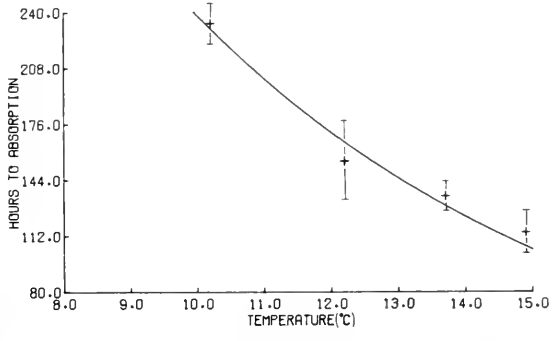

FIGURE 2.—Effects of temperature on 50% time to complete yolk-sac absorption for Pacific hake larvae and 95% confidence intervals. Data was fitted to a Gompertz curve: $Y = 1{,}269.52 * \exp(-108.82 * (1 - \exp(-0.0016 * X)))$.

TABLE 1.—Starvation experiments.

Temperature (°C)	Mean time to starvation (h)	Standard deviation	100% starvation (h)	No. of larvae
8	251.0	65.6	318	3
12	200.2	29.1	235	4
15	150.0	17.8	168	5

Growth Rates

Larvae were reared in the laboratory beyond the yolk-sac stage (±1 d) to verify otolith increments as daily marks. Increments begin to be added 1-2 d before complete yolk-sac absorption, perhaps coinciding with the onset of feeding; after yolk absorption, 1 ring is apparently added each day (Fig. 3). Rings on these otoliths were much fainter than those of field-caught specimens, possibly due to poor feeding, lighting, or other rearing conditions in the lab. Postyolk-sac larvae grown in the laboratory survived up to 10

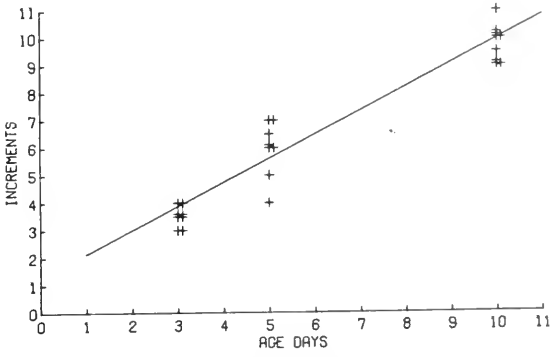

FIGURE 3.—The daily addition of increments by laboratory-reared postyolk-sac Pacific hake larvae.

d beyond the expected starvation date, but I was not able to maintain larvae much older than this.

The growth of field-caught larvae collected off California and stored in 80% ethanol was determined by otolith aging. Readings to 30 increments appear to clearly represent daily deposition of increments. However, after roughly 30 increments, dark bands appearing on the otoliths were separated by several inner rings and it was difficult to distinguish which were daily increments. R. Methot (Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, Calif.) who read many of these otoliths from large larvae, felt that the larger bands were the daily marks. For the large otoliths I read, I followed this assumption.

The growth of Pacific hake larvae in length (not corrected for preservation effects) was fitted with a Gompertz curve (Fig. 4); however, a straight line provides a better fit for larvae <20 d old (Fig. 4, insert). Pacific hake larvae grow slowly in length for at least the first 30 d of posthatching life and then grow rapidly.

Growth in weight was examined by determining a length-weight relationship for larvae (Fig. 5a) and then combining this information with the age-length relationship described above (Fig. 5b). The weights used were from larvae preserved in 80% ethanol and uncorrected for pres-

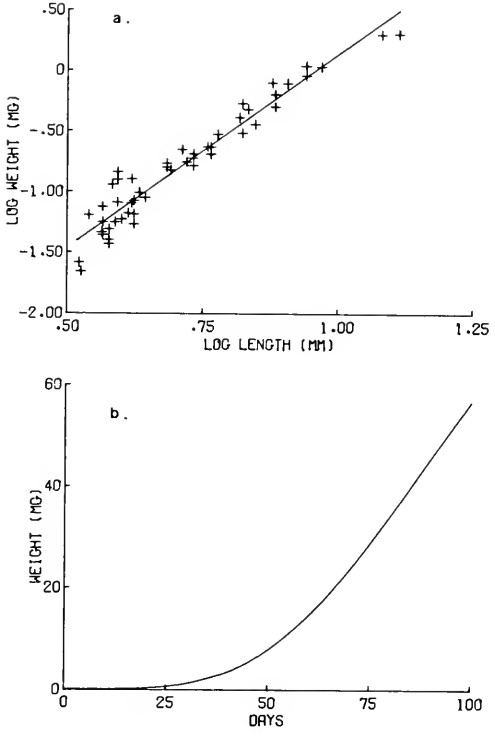

FIGURE 5.—Growth in weight of Pacific hake larvae. a. length-weight relationship of larvae off California (dry weights are from larvae preserved in ethanol), b. age-weight relationship.

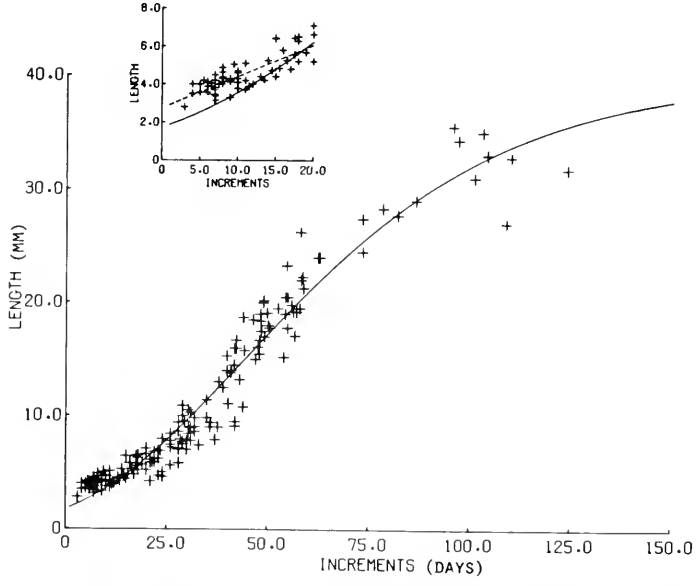

FIGURE 4.—The growth of larvae caught off southern California determined from otolith increments. A Gompertz curve was fit to the data, $Y = 1.72 * \exp(3.15 * (1 - \exp(-0.02624 * X)))$. Insert: daily growth for the first 20 d was fit better with a straight line: $Y = 2.75 + 0.16X$.

ervation effects. Increase in weight also appears to be slow for at least the first 30 d of posthatching life.

Weight loss of first-feeding larvae due to preservation in 80% ethanol was 57.8%, probably due mostly to loss of lipids and soluble proteins; weight loss in 3% Formalin was 24.1% (Table 2).

Shrinkage in length of first-feeding larvae preserved in Formalin was 8.9%; shrinkage of larvae preserved in ethanol was 3.6% (Table 3). Shrinkage due to delay in preservation was examined. Larvae in the 9-min delayed group decreased 17% in length, while those in the 29-min group decreased 40% in length. Most larvae, and especially larger larvae, probably do not die during the tow, and I have observed that in Puget Sound most larvae are alive after capture with a jar-type cod end. However, after a typical CalCOFI tow it probably takes an average of 5-10 min to remove and wash the cod end before preserving the larvae. I estimate that in routine sampling surveys small Pacific hake larvae probably shrink 9-20% in length due to handling. Shrinkage of large larvae was not tested and is probably different.

TABLE 2.—Weight loss due to preservation, determined by comparing fresh-frozen larvae to preserved larvae. Dry weights in milligrams.

	Live	80% ethanol	3% Formalin
Mean dry-weight (mg)	0.083	0.035	0.063
Standard deviation	0.007	0.004	0.006
No. of larvae	5	5	5
% of live weight	100.0	42.2	75.9

TABLE 3.—Shrinkage in standard length of first-feeding larvae due to preservative and related to delay in time of preservation, determined by comparing standard lengths of live larvae with preserved larvae. Three larvae per treatment; lengths are in millimeters.

	Ethanol	Formalin			
Preservative:	80%	3%	3%	3%	3%
Minutes delay	0	0	9	16	29
Mean live length	4.44	4.63	4.52	4.46	4.52
Mean fixed length	4.28	4.22	3.73	3.70	2.71
% length loss	3.6	8.9	17.5	17.0	40.1

Metabolic Rates

Respiration rates for Pacific hake larvae increase as a function of temperature and size (Fig. 6; Table 4). The experimental temperatures represent the range encountered by hake larvae within the spawning region. At 12°C, the mean temperature larvae experience off California,

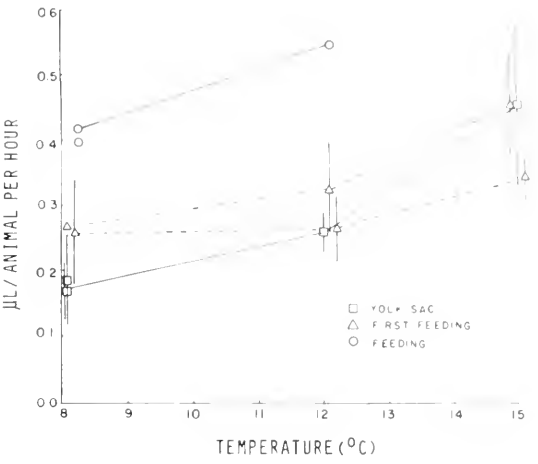

FIGURE 6.—The effect of temperature on mean respiration rates (µl/animal per h) of Pacific hake larvae of different stages. Vertical bars are ±1 standard deviation.

respiration rates for first-feeding larvae are 4.8-6.8 µl/mg-dry wt per h. These respiration rates were determined in 30 ml bottles, which did appear to slightly impair the swimming activity of larvae. Consequently, these rates are considered to be within the range between routine and active metabolism. The dry weights reported in Table 4 are of Formalin-preserved larvae, uncorrected for weight loss due to preservation. With the correction, weight specific rates would be 25% lower.

Vertical Distribution

Ahlstrom (1959) noted that Pacific hake eggs (and also most unsized hake larvae) were aggregated near the base of the mixed layer. From my analysis, most small larvae <8 mm were caught in the 50-100 m depth interval (Fig. 7), which corresponds to Ahlstrom's observations. Larger larvae were caught deeper; however, large larvae near the surface may be more able to avoid capture. An analysis by Lenarz (1973) indicates that larger larvae are probably able to avoid plankton nets in daytime. Large larvae, >12 mm, appear to be close to the surface later in the year (May-June), and have been caught at depths of only 25-50 m in nighttime plankton tows (A. Alvariño[3]). From my own observation in June

[3]A. Alvariño, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1979.

TABLE 4.—Summary of respiration experiments. Dry weights are of Formalin preserved larvae, uncorrected for weight loss due to preservation.

Temperature (°C)	Experiment	Mean length (mm)	Mean weight (mg)	Replicates	Larvae/jar	µl/animal per h	SD	µl/mg-dry wt per h
8	a. yolk sac	—	—	3	3	0.170	0.044	4.47
	b. yolk sac	3.49	0.038	3	5	0.185	0.072	4.87
	c. 1st feeding	3.81	0.049	2	2	0.271	—	5.53
	d. 1st feeding	3.97	0.055	4	3	0.260	0.083	4.73
	e. feeding	3.95	0.068	3	1	0.402	0.244	5.91
	f. feeding	3.97	0.070	2	1	0.426	—	6.09
12	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.261	0.027	6.87
	c. 1st feeding	3.81	0.049	3	2	0.332	0.066	6.78
	d. 1st feeding	3.97	0.055	3	3	0.265	0.052	4.82
	e. feeding	—	—	—	—	—	—	—
	f. feeding	3.97	0.070	2	2	0.549	—	7.84
15	a. yolk sac	—	—	—	—	—	—	—
	b. yolk sac	3.49	0.038	4	3	0.460	0.126	12.11
	c. 1st feeding	3.81	0.049	3	3	0.467	0.080	9.53
	d. 1st feeding	3.97	0.055	4	3	0.345	0.041	6.27
	e. feeding	—	—	—	—	—	—	—
	f. feeding	—	—	—	—	—	—	—

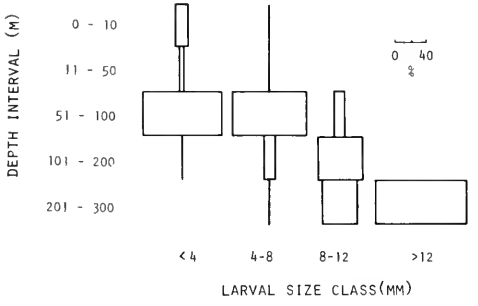

FIGURE 7.—The vertical distribution of Pacific hake larvae off the California coast shown as the percent of larvae within each depth interval by size class. Sample numbers are 1174, LT 4 mm; 1051, 4-8 mm; 19, 8-12 mm; 5, GT 12 mm; total sample of 2,249 larvae.

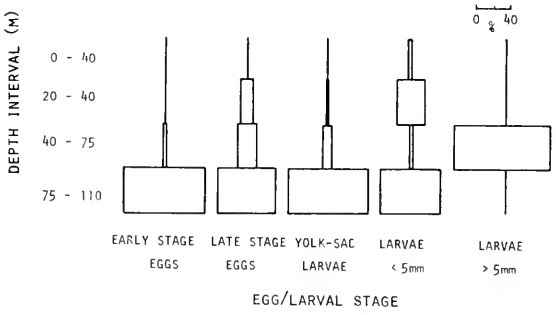

FIGURE 8.—The vertical distribution of Pacific hake eggs and larvae at Port Susan, Wash., shown as the percent of eggs or larvae within each depth interval by developmental stage or size class. Sample numbers: early stage eggs, 2,845; late stage eggs, 1,147; yolk-sac larvae, 409; larvae LT 5 mm, 31; larvae GT 5 mm, 12; total sample of 4,444.

1979, large larvae were also caught in midwater trawls near the surface in nighttime.

In contrast to eggs and larvae off the California coast, which are found at midwater, Pacific hake eggs and larvae in Puget Sound are located near the bottom of the water column. This is shown in Figure 8 for animals sampled at Port Susan (maximum depth, 110 m). This trend was also observed for animals collected at Dabob Bay (maximum depth, 175 m); the majority of eggs and larvae were found in the bottom 25 m of the water column. The difference in vertical distribution between eggs off California and eggs in Puget Sound may be explained as follows. The water at a reference level of 100 m is less saline (29.3‰) and less dense (1.0228) in Puget Sound than water off the California coast (33.6 ‰ 1.0258). Off California, eggs are spawned at 200-500 m depth, are relatively buoyant compared with the surrounding water, and rise upward to a level of equal buoyancy. Eggs in Puget Sound are spawned near bottom (Thorne 1977). Assuming that they are about the same density as the California eggs, these eggs are relatively less buoyant in the less dense water of Puget Sound, and therefore remain near the bottom.

DISCUSSION

Compared with eggs and larvae of other fishes in the California Current system, rates of development, growth, and metabolism of Pacific hake eggs and larvae are slow. These factors may be indicative of survival tactics (Hunter 1980), and differences could reflect the relative importance of certain environmental conditions, such as food abundance and predation pressure, in larval sur-

vival. Hunter (1980) contrasted several types of life history tactics for larvae of marine fishes. He indicated that in relatively cold water, where metabolic costs are low, a tactic of slow growth, feeding on large prey, and passive hunting may be common. This does appear to be the strategy of Pacific hake larvae. This tactic is quite different from that of high metabolism, fast growth, and active hunting demonstrated by other larvae, such as Pacific mackerel and to a lesser extent northern anchovy. Larvae of Pacific hake are located in colder water than larvae of Pacific mackerel and northern anchovy (Ahlstrom 1959) and compared with these other species the growth of Pacific hake larvae is slow (Fig. 9). Metabolic rates are difficult to compare because of different experimental techniques, but as a lower limit (due to the restrictive container size), 3-5 d old Pacific mackerel larvae require about 0.411 μl-O_2/animal per h at 19°C (Hunter and Kimbrell 1980). This compares with 0.265 μl-O_2/animal per h for first-feeding Pacific hake larvae at 12°C from this study.

I have calculated the energetic requirements of a first-feeding Pacific hake larva based on the routine metabolic rate at 12°C (the ambient temperature off the California coast) and growth in weight for larvae caught in the field, after correcting for preservation effects (Table 5). These values were converted to calories assuming values of 1 μl-O_2 = 0.005 cal and 1 mg-dry weight of

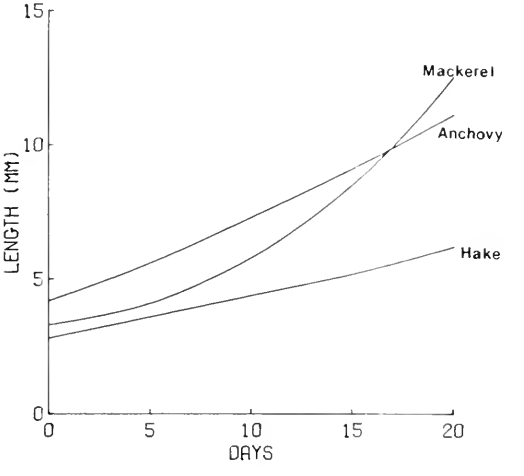

FIGURE 9.—Comparative growth of field-caught Pacific hake larvae (at 11°-14°C; this study), field-caught anchovy larvae (13°-16°C; Methot and Kramer 1979), and laboratory-reared Pacific mackerel larvae (19°-20°C; Hunter and Kimbrell 1980).

TABLE 5.—Caloric requirement of first-feeding Pacific hake larvae from growth and metabolism.

		Length (mm)	Weight (mg)	Corrected weight (mg)[1]
Respiration rate at 12°C = 0.30 μl/animal per h				
Growth:	day 4	3.412	0.0440	0.0694
	day 5	3.577	0.0512	0.0808
Weight gain = 0.011 mg/d = 0.0550 calories[2]				
Respiration = 7.20 μl/d = 0.0360 calories[3]				
			0.0910 calories	

Daily ration = Metabolism + Growth + Nonassimilated + Egestion
Daily ration × 0.7 = Metabolism + Growth
Daily ration = 0.130 calories

[1]Corrected for preservation effects
[2]5.003 cal/mg-dry wt tissue (Laurence 1977).
[3]0.005 cal/μl-O_2 (Laurence 1977)

larval fish tissue = 5.003 cal (Laurence 1977). The average first-feeding hake larva thus requires 0.091 cal/d to maintain and grow. This value is likely to be an underestimate of the caloric requirement due to an undetermined amount of energy needed to attack, capture, and digest prey animals. Estimates of assimilation coefficients range from 0.8 (Healy 1972; Dagg 1976) to 0.5 (Vlymen 1977). Assuming an assimilation coefficient of 0.7, as suggested by Ware (1975) and Laurence (1977), Pacific hake larvae would need to ingest 0.130 cal/d to satisfy metabolic and growth costs. Although this seems to be a reasonable estimate, significant errors may arise from the factors used for length-weight conversion, preservation effects, and from the assumed assimilation coefficient. I would suggest a more thorough examination of these factors in future experiments.

Using Sumida and Moser's (1980) report on the stomach contents of 3-4 mm Pacific hake larvae (Table 6), I calculated an estimate of daily ration that can be compared with the above estimate. Several approximations are necessary in this calculation, including 1) a feeding period of 12 h, 2) a digestion time, which I assume to be 5 h—ranges for other species are 3-8 h for herring (Werner and Blaxter 1980) and 2-4 h for Pacific mackerel (Hunter and Kimbrell 1980), and 3) a value of 5.2519 cal/mg-dry wt for copepods (Laurence 1976). The daily ration can then be calculated as: Daily ration = Stomach content weight × Feeding period/Digestion time (Feigenbaum 1979; Laurence 1977). For small Pacific hake larvae the daily ration thus calculated is 0.129 cal, which compares very closely with the previous estimate.

Hunter and Kimbrell (1980) calculated that 3-5 d old Pacific mackerel larvae require 0.143 cal/d to maintain and grow, based on the weight

TABLE 6.—Average daily ration of 3-4 mm Pacific hake larvae (data from Sumida and Moser 1980, table 1). Number prey/stomach includes those with empty guts.

Prey organism	Total length (mm)[1]	Prosome length (mm)[2]	Dry weight (mg)[3]	No. prey/ stomach	Dry weight/ stomach (mg)
Adults					
Clausocalanus	1.15	0.70	0.006	0.38	0.00228
Paracalanus	1.0	0.57	0.004	0.29	0.00116
Calocalanus	1.0	0.57	0.004	0.08	0.00032
Oithona	0.95	0.52	0.003	0.03	0.00009
Calanoid unid	1.04	0.60	0.004	0.09	0.00036
Disintegrated	1.04	0.60	0.004	0.08	0.00032
Copepodites					
Calanus sp.	1.50	1.00	0.050	0.02	0.00100
Oithona			0.002	0.03	0.00006
Calanoid			0.002	1.09	0.00218
Cyclopoid			0.002	0.03	0.00006
Disintegrated			0.002	0.21	0.00042
Nauplii			0.001	2.00	0.00200
Eggs			0.0005	1.06	0.00056
					0.01025

Calories per stomach = 0.01025 mg × 5.2519 cal/mg-dry wt[4] = 0.05383 cal.

$$\text{Daily ration} = \frac{\text{Calories in stomach} \times \text{Feeding period}}{\text{Digestion time}} \quad \text{(Feigenbaum 1979, Laurence 1977)}$$

$$= \frac{0.0538 \times 12}{5} = 0.129 \text{ cal/d}$$

[1]From Brodskii 1967, Fulton 1968.
[2]From Total length = 1.16 × prosome length + 0.34; Fulton 1968.
[3]From Vidal 1978; Feigenbaum 1979.
[4]5.2519 cal/mg-dry weight conversion for copepods (Laurence 1976).

gain of laboratory-reared larvae and metabolic rates at 19°C. As they note this must be a lower limit. Assuming the same assimilation coefficient that I used for hake, 0.7, mackerel would need to ingest 0.204 cal/d to satisfy this ration requirement. First-feeding hake larvae have very large mouths compared with either mackerel or anchovy (Fig. 10), so they may feed on a wide size range of planktonic animals (including adult copepods); hake larvae could satisfy daily rations by capturing 25 nauplii or 15 small copepodites or 6 small calanoid adults or 1 *Calanus* adult. In contrast, both first-feeding mackerel and anchovy require a smaller size range of food particles (Hunter 1980). At least for anchovy, their survival depends on finding patches of small food organisms, such as the dinoflagellate, *Gymnodinium* (Lasker 1975). To satisfy its ration requirement a first-feeding Pacific mackerel larva would have to capture 4,000 *Gymnodinium* cells, 240 rotifers, or 39 copepod nauplii. It seems evident that they require high density patches of prey for successful feeding, whereas hake larvae may not require such dense patches of food for successful first-feeding.

From the results of this study, I infer that the first feeding of Pacific hake larvae is not as important to their survival as it is for Pacific mackerel and also for northern anchovy. This concept is supported by 1) the lower daily ration of hake larvae due to temperature-dependent activity and growth, 2) larger food items in the diet of hake larvae which provide more calories per prey item, 3) the relatively longer starvation time for hake larvae, i.e., they take 6-12 d to starve after complete yolk utilization, whereas anchovy take only about 4 d (Lasker et al. 1970), and 4) the ability of hake larvae to feed while still having yolk reserves (Sumida and Moser 1980). In addition, there is evidence of high energy wax esters in eggs of *Merluccius* (Mori and Saito 1966); thus larvae may have a longer safety period to find food. This concept does not exclude the possibility of a critical starvation period occurring later in larval or postlarval life, when stored energy reserves are exhausted and energetic demands are greater.

Predation may be relatively important as a factor influencing survival of Pacific hake larvae. Egg and yolk-sac stages of marine fish appear to be the stages most vulnerable to predation (Theilacker and Lasker 1974; Hunter 1980). Because of the colder temperatures that Pacific hake eggs and larvae inhabit, and resulting growth and development rates that are slow compared with Pacific mackerel (Hunter and

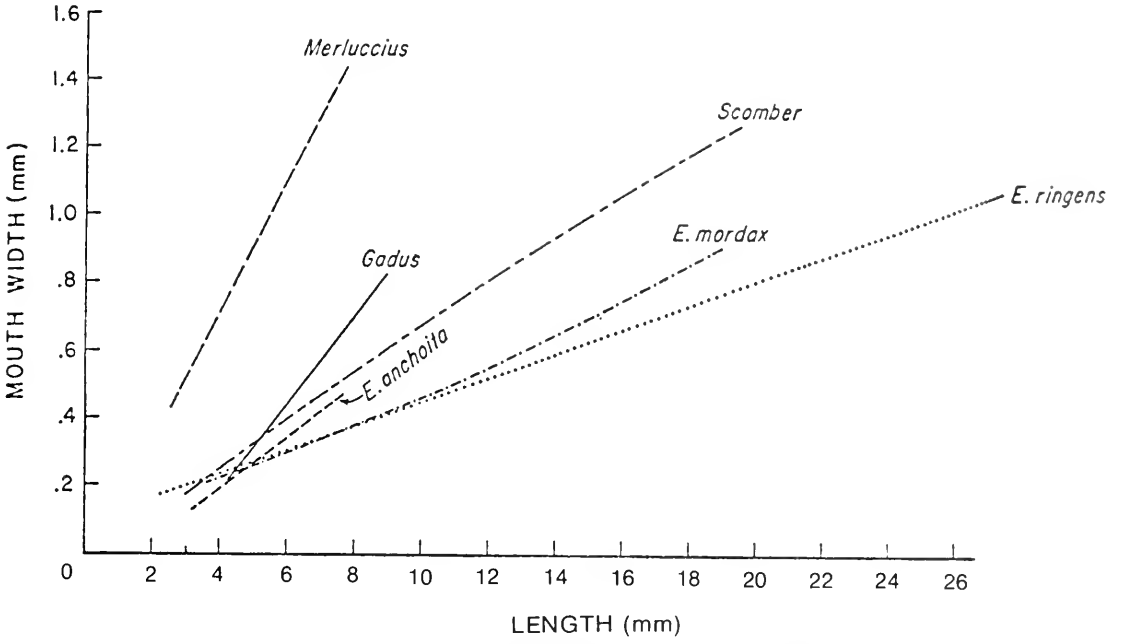

FIGURE 10.—Mouth sizes of larvae of hake, mackerel, anchovy, and cod by length class (Hunter 1980).

Kimbrell 1980) and northern anchovy (Zweifel and Lasker 1976), Pacific hake spend a longer time in vulnerable stages. Consequently, predation pressure on hake eggs and larvae may be high.

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THE BIOLOGY OF THE WHITE PERCH, *MORONE AMERICANA*, IN THE HUDSON RIVER ESTUARY

D. W. BATH AND J. M. O'CONNOR[1]

ABSTRACT

White perch, *Morone americana*, are found throughout a 250 km region in the Hudson River from Manhattan north to Albany, New York. They represent a dominant species in most portions of the river, although they are of little importance in the commercial fishery. Life history information was determined for more than 7,500 white perch collected from a 15 km region of the Hudson River between Haverstraw and Bear Mountain, New York.

Annulus formation began by the first week in May and was completed by the end of July. Maximum age for both male and female white perch was 7 years. Most of the growth occurred in the first 3 years for both males and females, and represented 78% of the length attained by the seventh year. Most fish were sexually mature by their second year. The length-weight relationship observed for Hudson River white perch was Log $W = -4.743 + 3.093$ Log L. The mean fecundity was 50,678 eggs per female, with a range of 15,726-161,449.

The white perch, *Morone americana* (Gmelin), inhabits rivers, bays, and estuaries of the Atlantic coast from Nova Scotia to South Carolina (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Leim and Scott 1966). The species has been introduced to freshwater lakes and reservoirs through migration, stocking, and by being landlocked in impoundments (Bigelow and Schroeder 1953; Mansueti 1961; Woolcott 1962). White perch has been reported in Lake Ontario (Sheri and Power 1969), Lake Erie (Larsen 1954; Trautman 1957), and the waters of Quebec (Scott and Christie 1963; Leim and Scott 1966). Most recently it has been introduced into the waters of Nebraska (Hergenrader and Bliss 1971).

White perch is found throughout a 250 km region in the Hudson River from Manhattan north to Albany, N.Y. It represents a dominant species in most portions of the river (McFadden[2]), although it is of little importance in the commercial catch (Sheppard[3]). The species is particularly abundant in the Hudson River from Nyack north to Catskill, N.Y. (Perlmutter 1967).

With the exception of a fecundity study (Holsapple and Foster 1975), no life history information for white perch in the Hudson River has been published. Site-specific data for white perch populations are available in reports (Raytheon Co.[4]; Lawler, Matusky and Skelly Engineers[5, 6]; Texas Instruments Inc.[7]). The present study was carried out to investigate the life history of white perch in the Hudson River estuary over a 15 km section, from Haverstraw to Bear Mountain, N.Y. This section of the Hudson River is a very stressful environment owing to frequent changes in salinity: On an annual basis, the region experiences one to several transitions between limnetic and oligohaline conditions (Abood 1974). The white perch is one of the highly adaptable species that can tolerate these changes. Along with the hogchoker, *Trinectes maculatus*, it is a dominant year-round resident of this portion of the Hudson region.

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[2]McFadden, J. T. 1978. Influence of the proposed Cornwall pumped storage project and steam electric generating plants on the Hudson River Estuary with emphasis on striped bass and other fish populations. Rep. for Consolidated Edison Co. of N.Y., Inc., 1179 p.

[3]D. J. Sheppard, New York State Department of Environmental Conservation, 50 Wolfe Road, Albany, NY 12223, pers. commun. March 1980.

[4]Raytheon Co. 1971. Indian Point ecological survey report II, January-June 1970. Submarine Signal Div., Portsmouth, R.I., 165 p.

[5]Lawler, Matusky and Skelly Engineers. 1974. Hudson River aquatic ecology studies at Roseton and Danskammer Point. Vol. III. Fish. Rep. to Central Hudson Gas and Electric Corp., N.Y., 114 p.

[6]Lawler, Matusky and Skelly Engineers. 1974. Hudson River aquatic ecology studies—Bowline Point and Lovett Generating Stations. Vol. IV, 445 p.

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MATERIALS AND METHODS

We collected white perch at seven beach seining stations, nine trawling areas, and one experimental mesh gill net location between Haverstraw and Bear Mountain, N.Y., on the Hudson River from April through November 1970 (Fig. 1). Beach seine collections were made with a 30.4 m by 2.4 m seine (9.5 mm square mesh) or a 15.2 m by 1.5 m seine (6.5 mm square mesh), each with a central bag of 6.5 mm square mesh. The large seine was set from shore with the aid of a boat and retrieved in a semicircle. The 15.2 m seine was handhauled by pulling the seine parallel to the shore in water ~1.2 m deep. The large seine was fished in water ~2.4 m deep.

Bottom and surface trawls were made with a 7.6 m semiballon trawl, constructed with a 38.1 mm stretch mesh nylon body, with a 31.8 mm stretch mesh nylon cod end rigged with an inner liner of 6.5 mm stretch mesh nylon. Trawl doors were 1.1 m in length and 0.46 m in width. Tow

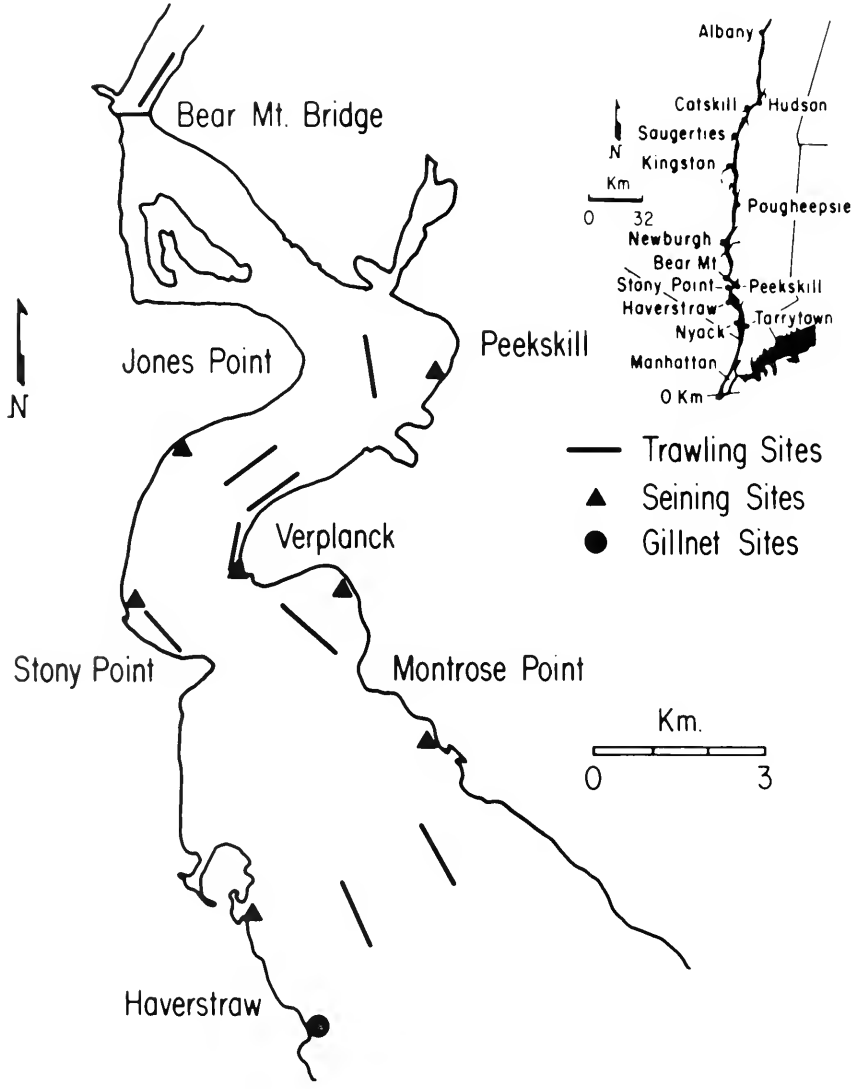

FIGURE 1.—Region of Hudson River from which white perch were collected.

speed for trawling was about 3.4 km/h. Details of the towing procedure are described in Bath et al. (1979).

The gill net was an experimental type with four panels of varying mesh size. The net measured 30.4 m by 1.8 m and contained 7.6 m each of 12.7, 25.4, 38.1, and 76.2 mm stretch mesh monofilament line. It was hung from 9.5 mm braided, polycore float line, with a bottom lead-coreline.

All fish collected at each site were immediately labeled and preserved in 10% Formalin[8] and returned to the laboratory for analysis. Each fish was measured (standard length (SL)) to the nearest millimeter, weighed to the nearest 0.1 g, and the sex was determined. A subsample of 310 fish was measured for fork length (FL) and total length (TL) to determine regression equations for comparison of Hudson River white perch populations with data from other river systems. Mature ovaries and testes were removed from selected individuals, weighed, and preserved in 10% Formalin. The ovaries were later transferred to Gilson's fluid for fecundity analysis (Ricker 1968). Stomachs were removed from randomly selected fish and preserved in 10% Formalin for later food analysis. Scales for age analysis were removed from behind the left pectoral fin (Rounsefell and Everhart 1953), cleaned, pressed, and sealed between glass microscope slides. The scales were read within 6 mo of the collection date.

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

RESULTS

Time of Annulus Formation

Annulus formation began by the first week in May and was completed in all age groups by the end of July (Table 1). Younger fish (age groups 1 and 2) completed the annulus by the end of June.

TABLE 1.—Percentage of aged white perch, *Morone americana*, with a new annulus and with a given number of circuli beyond the new annulus during a given period.

Date collected	Age (winters of life)	No spec.	Percent with new annulus	Percent with noted no of circuli beyond new annulus					
				0	1-2	3-4	5-6	7-8	>8
May 22-	1	11	73	64	9	0	0	0	0
June 2	2	36	50	50	0	0	0	0	0
(incl.)	3	36	39	39	0	0	0	0	0
	4	14	29	29	0	0	0	0	0
	5	14	0	0	0	0	0	0	0
	>5	31	0	0	0	0	0	0	0
June 9-	1	7	100	14	14	29	14	29	0
June 16	2	20	70	45	15	10	0	0	0
(incl.)	3	17	47	41	0	6	0	0	0
	4	14	43	22	14	7	0	0	0
	5	13	39	31	8	0	0	0	0
	>5	21	0	0	0	0	0	0	0
June 19-	1	5	100	0	0	0	40	20	40
June 30	2	7	100	29	14	57	0	0	0
(incl.)	3	8	50	50	0	0	0	0	0
	>3	9	33	33	0	0	0	0	0
July 1-	1	3	100	0	0	0	0	0	100
July 17	2	8	100	0	25	13	50	13	0
(incl.)	3	17	88	24	35	29	0	0	0
	4 or 5	6	83	67	16	0	0	0	0
	>5	5	20	0	0	0	0	0	0
July 24-	1	4	100	0	0	0	0	0	100
July 30	2	10	100	0	0	0	20	20	60
	3 or 4	7	100	43	57	0	0	0	0
	>4	2	100	100	0	0	0	0	0
Aug. 1-	1	10	100	0	0	0	0	0	100
Aug 15	2	21	100	0	0	0	10	14	76
	3	9	100	0	11	33	33	11	11
	4 or 5	12	100	8	17	58	17	0	0
	>5	2	100	50	50	0	0	0	0
Aug 17-	1	15	100	0	0	0	0	0	100
Aug 31	2	4	100	0	0	0	25	0	75
	3	6	100	0	0	17	50	0	33
	>3	6	100	0	17	67	17	0	0
Sept.-	1	15	100	0	0	0	0	0	100
Oct	2	5	100	0	0	0	0	0	100
	3	6	100	0	0	0	17	17	67
	>3	2	100	0	0	0	100	0	0

White perch of age groups 3 and older completed the annulus ~2 wk later.

Length-Frequency and Age Distribution

During May and June, there were three modes in the length-frequency data, with peaks at 65.0-69.0, 105.0-109.0, and 140.0-144.0 mm (Figs. 2, 3). These peaks represent the 1-, 2-, and 3-yr age groups. From July to November the length frequencies ranged from 10.0-14.0 mm to 200.0-204.0 mm (Fig. 4). The prominent mode at 50.0-54.0 mm represents young-of-the-year fish (Fig. 5).

Growth

The relationship between anterior scale radius and standard length for white perch from all age groups was $L = 32.64 + 45.56\,(R)$, where L = standard length in millimeters and R = scale radius in millimeters. The coefficient of determination (r^2) was 0.88 (Fig. 6).

The standard lengths at the various annuli were back-calculated and the growth histories were constructed for each year class, along with growth increments for each age group (Tables 2, 3). The most rapid growth occurred in the first 3 yr of life, and accounted for 78.0% of the total growth at the maximum size observed. Subsequent average growth increments were uniform among year classes, but considerably smaller (Fig. 7). Similar growth histories were compiled for each year class for both male and female white perch (Tables 4-7). Females grew slightly larger in TL than males of the same age (Fig. 8).

Length Conversions

We calculated the relationship between total length, fork length, and standard length measurements taken on a subsample of 310 white perch, ranging in size from 30.0 mm to 182.0 mm SL. A linear regression was computed to obtain conversions between the three methods so that we could compare growth rates among the different white perch studies. (Fig. 6). The relationship between total length and standard length was $SL = -1.05 + 0.81\ TL$, $r^2 = 1.0$; the relationship between fork length and standard length was $SL = -0.99 + 0.86\ FL$, $r^2 = 1.0$.

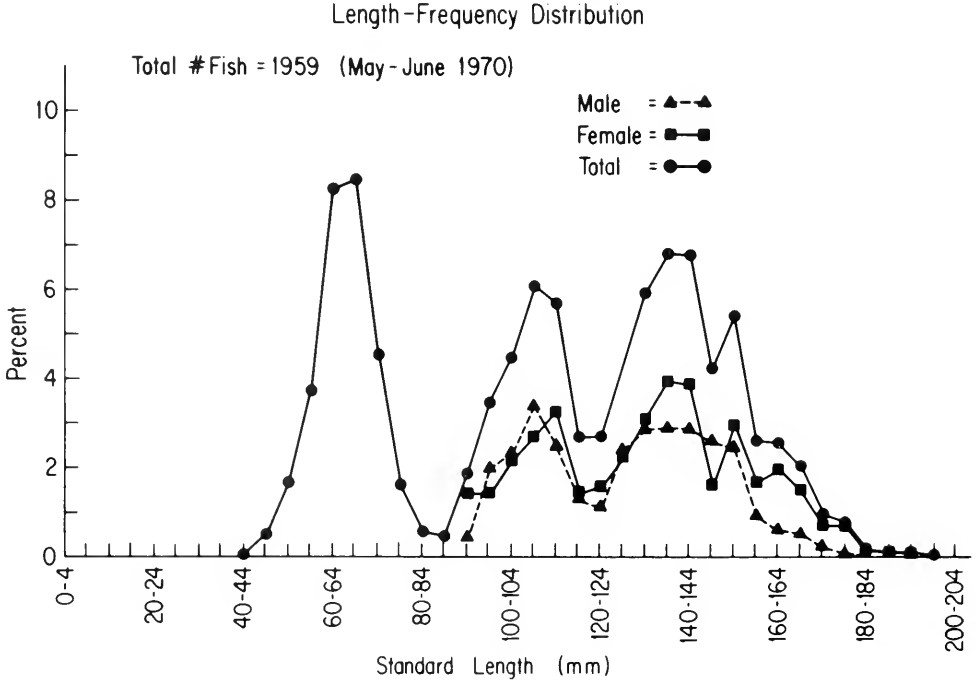

FIGURE 2.—Length-frequency distribution of white perch during May and June 1970, and for mature males and females during this same period.

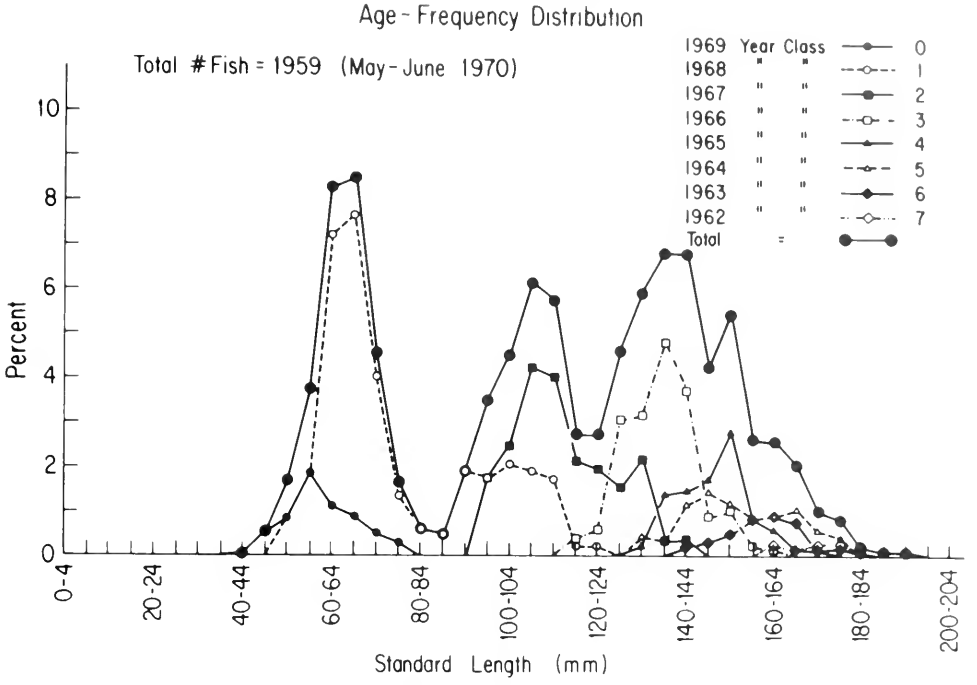

FIGURE 3.—Age-frequency distribution of white perch during May and June 1970.

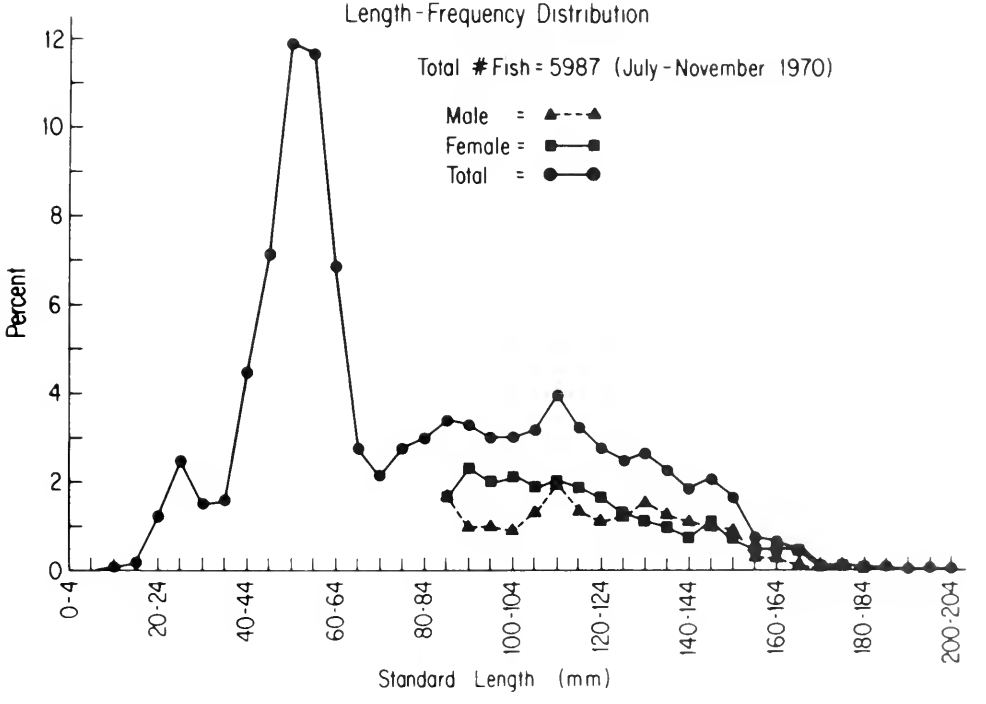

FIGURE 4.—Length-frequency distribution of white perch during July to November 1970, and for mature males and females during this same period.

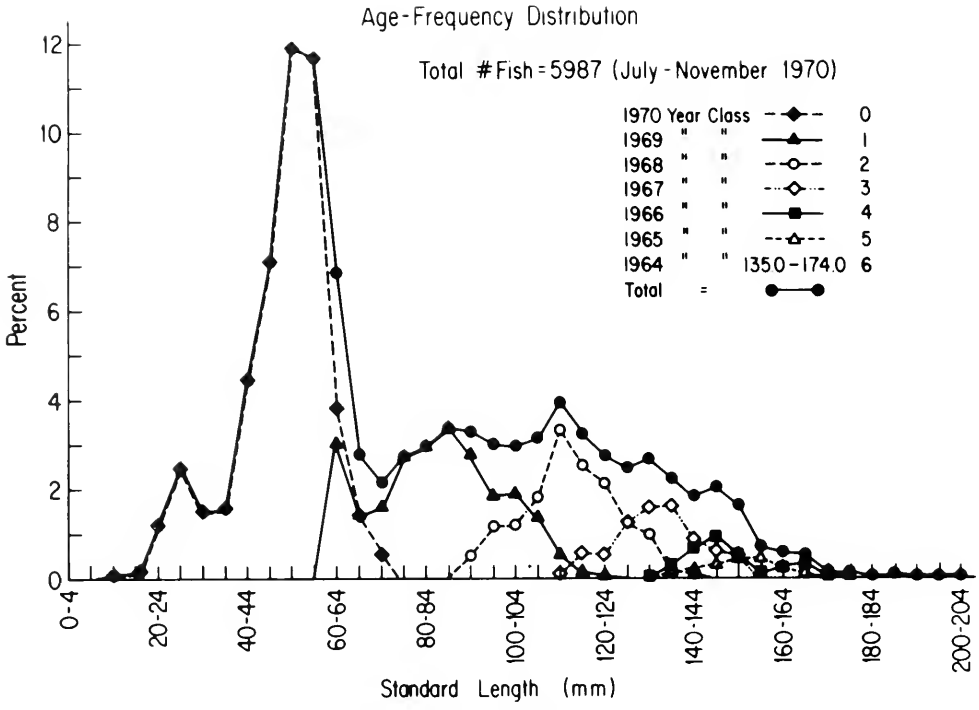

FIGURE 5.—Age-frequency distribution of white perch during July to November 1970.

TABLE 2.—Calculated growth of white perch in the Hudson River between Haverstraw and Bear Mountain, N.Y. (sexes combined), 1963-69.

Year class	No.	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	12	69.2	119.2	150.1	164.2	176.2	185.9	194.1
1964	36	71.9	122.6	150.8	164.2	174.9	184.5	
1965	68	68.9	119.2	148.4	164.2	177.7		
1966	85	70.2	121.6	150.6	167.6			
1967	139	69.4	123.5	153.9				
1968	219	71.7	126.6					
1969	243	80.1						
Weighted mean		73.4	123.8	151.5	165.6	176.6	184.8	194.1
Increment		73.4	50.4	27.7	14.1	11.0	8.2	9.3
Percent of total growth		37.8	26.0	14.2	7.2	5.6	4.2	4.8
No.		802.0	559.0	340.0	201.0	116.0	48.0	12.0

Length-Weight Relationship

The length-weight relationship for Hudson River white perch was calculated using the least squares method (Ricker 1968). The relationship for males was Log $W = -2.262 + 1.925$ Log L, $r^2 = 0.706$. For females, the relationship was Log $W = -4.738 + 3.099$ Log L, $r^2 = 0.965$. The combined male and female length-weight relationship was Log $W = -4.743 + 3.093$ Log L, $r^2 = 0.952$. The values of the exponents 1.925 and 3.099 indicate females were heavier than males of the same length ($F_{1,20} = 4.97$; $\alpha = <0.05$). Graphically expressed (Fig. 9), it can be seen that this occurred for females over 140.0 mm (age group 2+ and older) and can be related to fatness and gonad development (Le Cren 1951).

Reproduction

Sixty-five female white perch collected during May and June (115.0 to 187.5 mm SL) and representing age groups 2 to 7 were analyzed for fecundity. An exponential curve was fitted to

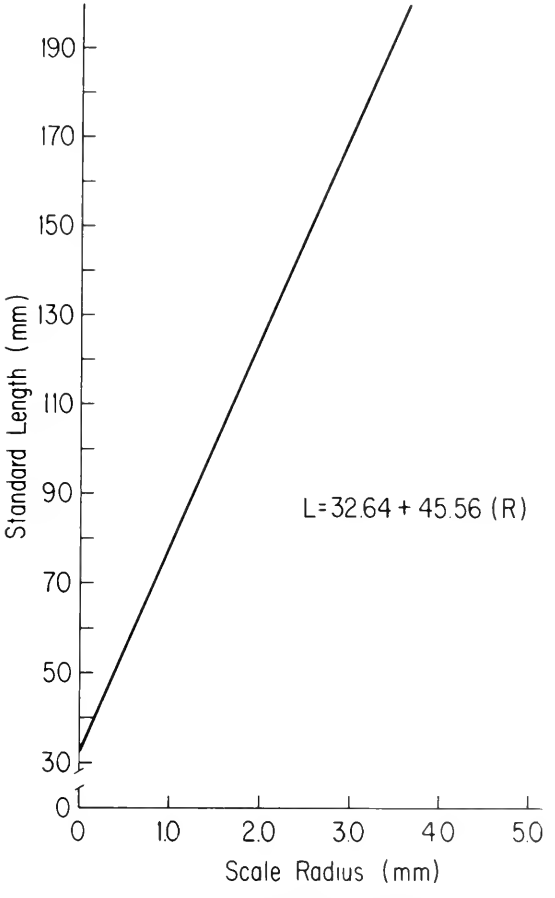

FIGURE 6.—Relationship between scale radius and standard length of white perch from the Hudson River between Nyack and Bear Mountain, N.Y. $r^2 = 0.88$.

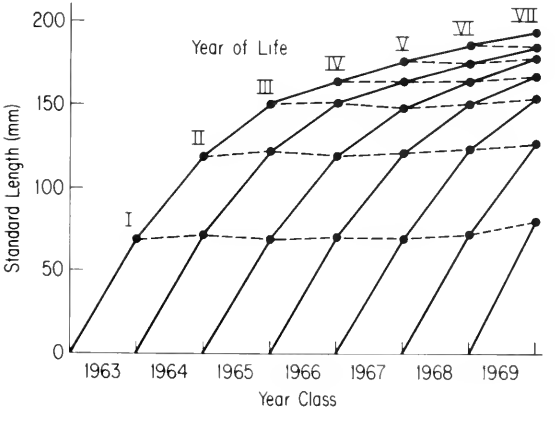

FIGURE 7.—Graphic representation of the growth histories of year classes of white perch from the Hudson River between Nyack and Bear Mountain, N.Y., 1963-69.

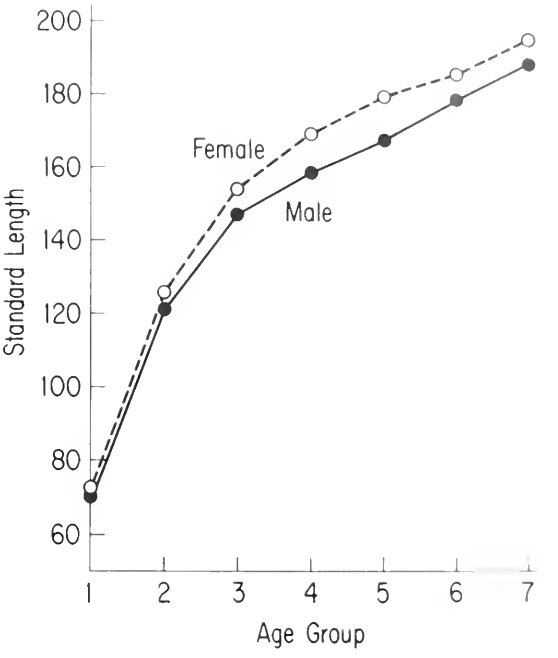

FIGURE 8.—Mean calculated standard lengths (mm) and increments of growth for each year of life of white perch from the Hudson River between Nyack and Bear Mountain, N.Y.

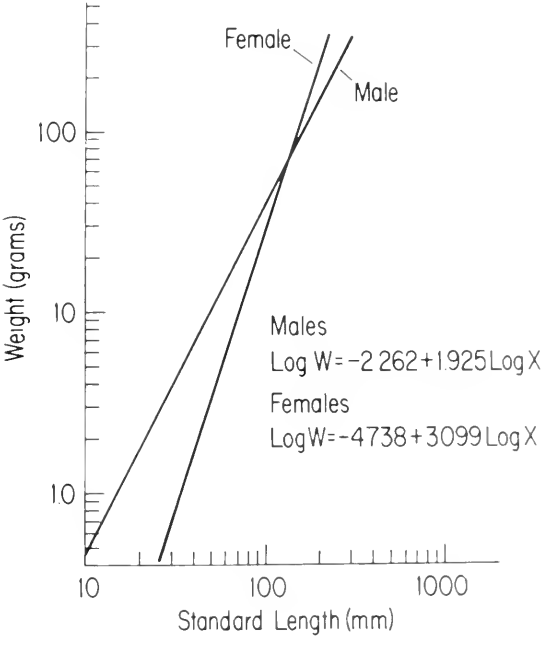

FIGURE 9.—Length-weight relationships of male and female white perch from the Hudson River between Nyack and Bear Mountain, N.Y. For males, $r^2 = 0.706$; for females, $r^2 = 0.965$.

fecundity data for May and June (Fig. 10). The egg-to-length relationship was $Y = 1{,}697.08e^{0.02X}$, where Y = number of eggs per fish and X = length, $r^2 = 0.39$. The white perch analyzed had a mean fecundity of 50,678 eggs/female with a range of 15,726-161,449.

The relationship between ovary weight and total body weight for 243 female white perch of known age collected from May to October is shown in Table 8. The changes in the ratio of ovary weight to body weight expressed as a percentage shows that spawning took place during June and was completed by July. Thereafter the ovaries are refractory and do not regain their weight until prior to the succeeding spawning season. The occurrence of the spawning season is further substantiated by the occurrence of white perch eggs and larvae in ichthyoplankton during June and July collections from the Hudson River (Lauer et al. 1974).

TABLE 3.—Growth history of the white perch in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for indicated year of life						
	1	2	3	4	5	6	7
1963	69.2						
1964	71.9	50.0					
1965	68.9	50.7	30.9				
1966	70.2	50.3	28.2	14.1			
1967	69.4	51.4	29.2	13.4	12.0		
1968	71.7	54.1	29.0	15.8	10.7	9.7	
1969	73.4	54.9	30.4	17.0	13.5	9.6	8.2

TABLE 4.—Calculated growth of white perch males in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Year class	No.	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	2	66.9	115.2	142.3	156.8	169.3	179.7	189.1
1964	11	68.2	117.2	144.9	157.0	168.5	178.9	
1965	32	66.5	114.3	140.2	155.2	167.2		
1966	37	69.3	119.4	146.6	162.6			
1967	54	68.6	121.6	152.5				
1968	63	70.6	126.2					
1969	21	79.4						
Weighted means		70.0	121.2	147.2	158.8	167.6	179.0	189.1
Increment		70.0	51.2	26.0	11.6	8.8	11.4	10.1
Percent of total growth		37.0	27.1	13.8	6.1	4.6	6.0	5.3
No.		220.0	199.0	136.0	82.0	45.0	13.0	2.0

TABLE 5.—Growth history of the white perch males in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for indicated year of life						
	1	2	3	4	5	6	7
1963	66.9						
1964	68.2	48.3					
1965	66.5	49.0	27.1				
1966	69.3	47.8	27.7	14.5			
1967	68.6	50.1	25.9	12.1	12.5		
1968	70.6	53.0	27.2	15.0	11.5	10.4	
1969	70.0	55.6	30.9	16.0	12.0	10.4	9.4

Sex Ratio

Of the 2,600 mature fish collected, 1,209 were males and 1,442 were females, giving an overall sex ratio of 0.83 to 1.0 in favor of females. This phenomenon has been observed for other fish populations in which females attain an older age

TABLE 6.—Calculated growth of white perch females in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Year class	No	Calculated standard length (mm) at end of year						
		1	2	3	4	5	6	7
1963	10	69.6	120.1	151.9	166.2	177.6	187.6	195.8
1964	25	73.2	124.4	151.4	165.8	175.6	185.6	
1965	29	70.4	121.9	152.8	170.1	183.8		
1966	41	70.6	123.2	154.6	171.7			
1967	67	70.5	125.6	156.2				
1968	98	73.0	128.6					
1969	35	78.8						
Weighted means		72.4	125.6	154.2	169.3	179.6	186.2	195.8
Increment		72.4	53.2	28.6	15.1	10.3	6.6	9.6
Percent of total growth		36.9	27.2	14.6	7.7	5.2	3.4	4.9
No.		305.0	270.0	172.0	105.0	64.0	35.0	10.0

TABLE 7.—Growth history of white perch females in the Hudson River between Haverstraw and Bear Mountain, N.Y., 1963-69.

Growth period	Growth increment for year of life						
	1	2	3	4	5	6	7
1963	69 6						
1964	73 2	50 5					
1965	70 4	51 2	31 8				
1966	70 6	51 5	27 9	14 3			
1967	70.5	52 6	30 9	14 4	11 4		
1968	73.0	55 1	31 4	17 3	9 8	10 0	
1969	72 4	55 6	30 6	17 1	13 7	10 0	8 2

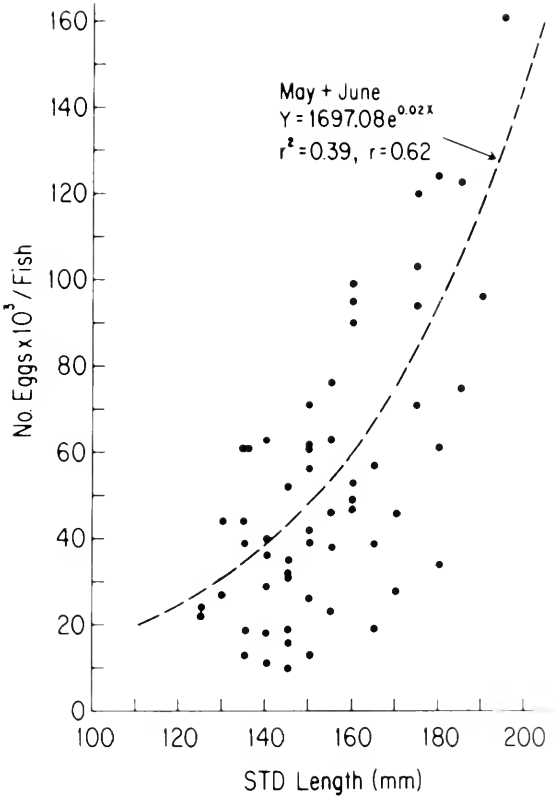

FIGURE 10.—Relationship between fecundity and standard length in female white perch collected during May and June from the Hudson River between Nyack and Bear Mountain, N.Y.

TABLE 8.—Mean ovary weight expressed as percentage of body weight.

Age	May	June	July	August	September	October
2	4 0	3 6	1 1	0 5	0 4	1 1
3	4 7	4 3	1 8	0 4	0 6	0 7
4	7 1	4 0	1 0	0 5	—	1 8
5	5 9	3 9	1 5	0 8	—	—
6	5 9	4 1	0 6	—	—	—
7	7 8	3 0	—	0.5	—	—

Total no. of fish 243

than males (Elrod and Hassler 1969). Chi-square analysis of data from individual collections showed the difference to be significant ($\chi^2 = 132.1$; $P<0.001$). During May and June the population consisted of 70.1% mature males and females and 29.9% immature fish. From July to November the population consisted of 40.6% mature males and females and 59.4% immature fish. The change observed in the population between mature and immature individuals was due to the recruitment of young-of-the-year fish into the population sampled by our gear.

DISCUSSION

The growth and reproductive characteristics of white perch from the Hudson River compare favorably with data from other riverine systems. The maximum age attained in the Hudson River is about 7 yr, and maximum size is about 200 mm. Other data from the Hudson River (Lawler, Matusky and Skelly Engineers footnote 6; Texas Instruments Inc. footnote 7) show maximum age to be 7 and 9 yr, respectively, with a maximum size of from 200 to 222 mm. White perch from the Connecticut River, Conn. (Marcy 1976; Marcy and Richards 1974) attained a maximum age of about 8 yr, but grew to a maximum size of more than 280 mm. Wallace (1971) and Miller (1963) studied brackish water segments of the Delaware River estuary white perch populations and reported maximum ages of 8 and 10 yr, respectively. However, Wallace obtained a maximum size (~175 mm) smaller than found in Miller's (~257 mm) and smaller than in other riverine populations. White perch from the Patuxent River, Md., and the Roanoke River, N.C., had a greater maximum age, up to 10 yr; however, the size attained at 7 yr is approximately the same as in the Hudson River, from 190 mm to 205 mm (Conover 1958; Mansueti 1961). In Figure 11 we have plotted calculated standard lengths by age groups for white perch from five riverine systems. A similarity of growth rates for most populations is obvious except for the Connecticut River where perch grow more rapidly throughout their life span. Such rapid growth is more characteristic of white perch in freshwater impoundments than of riverine populations (Thoits 1958).

The rapid growth of perch in the Connecticut River may be attributed to a longer growing season; the onset of annulus formation occurs nearly 2 mo earlier than in the Hudson River. However,

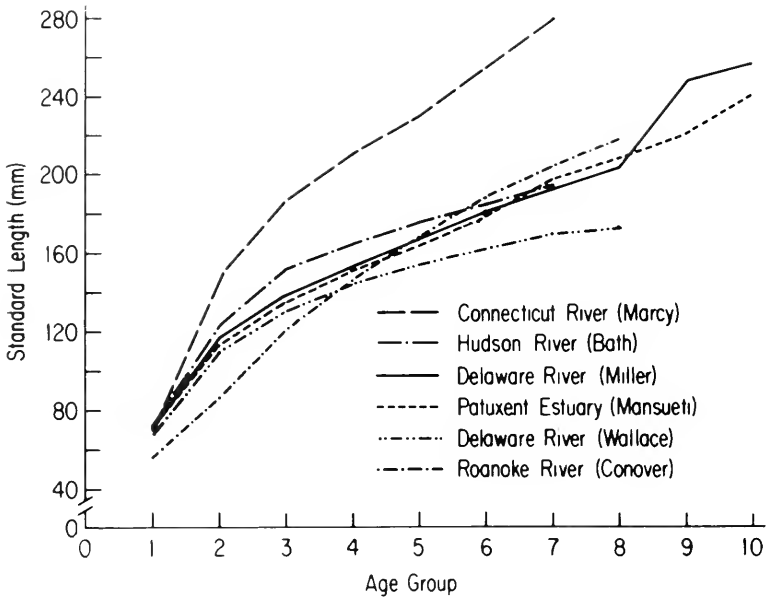

FIGURE 11.—Mean calculated standard lengths for white perch based on present and other studies.

this rapid growth rate estimate could be an artifact. Data from more recent year classes (1963-65) show lower rates of growth than observed from the 1959 through 1962 year classes (Marcy and Richards 1974). The Connecticut River population may be expanding rapidly and responding to increased population size with reduced rates of growth (Mansueti 1961).

White perch populations from south of the Hudson River show earlier onset and completion of the annulus. In the Chesapeake region, annulus formation begins in April (Mansueti 1961). In the estuarine portions of the Delaware River (Wallace 1971), the timing of annulus formation was shown to be complete by mid-June to early July. Lawler, Matusky and Skelly Engineers (footnote 5) reported that annulus formation in white perch from the Newburgh, N.Y., region of the Hudson River began in May and was completed by early July, essentially the same time observed in the present study. In Lake Ontario (Sheri and Power 1969) annulus formation was completed in July. The Connecticut River white perch (Marcy and Richards 1974) were anomalous in the apparent phenological trend of annulus formation, beginning in late March with completion during mid-May. This anomaly may be due to slightly higher average seasonal temperatures in the Connecticut River compared with those in the Hudson and Delaware Rivers, or it may be related to the fact that Marcy and Richards' (1974) studies were apparently carried out on a rapidly expanding population.

The basic reproductive potential for white perch, expressed as fecundity, appears to vary among the estuarine and freshwater populations studied. In estuarine and tidal rivers, fecundity values are similar throughout the range. White perch from the Roanoke River and Albemarle Sound, N.C., for example, had a mean fecundity of ~56,000 eggs/fish for age groups 3 and 4 (range 20,000-90,000; Conover 1958). Thoits (1958), in a generic study of white perch, estimated fecundity at 40,000 eggs/female. Hudson River fish fall close to this mean, with fecundity from three independent studies given as 21,000-135,000 (age groups 3 and 4; Holsapple and Foster 1975), 39,000-116,000 (Lawler, Matusky and Skelly Engineers footnote 6), and 16,000-161,000 with a mean of ~51,000 eggs/female in the present study. Variations in the data are most likely related to numbers of females sampled and the difficulty of obtaining fecundity data from a species which spawns over an extended period of time (Thoits 1958; Mansueti 1961; Taub 1969).

Freshwater lake populations of white perch may produce more eggs than similar groups in estuarine and tidal river systems. Au Clair (1956)

estimated the fecundity of white perch from Sebasticook Lake, Maine, at 164,000 eggs/female. Taub (1969), studying white perch from Quabbin Reservoir, Mass., gave a mean fecundity value of 271,000 eggs/female for age groups 3 and 4 (range 190,000-321,000). These fecundities, which are at least double that found in riverine populations, may be related to environmental factors such as food supply, sample size, time of capture, or technique used (Taub 1969). Growth data for these populations show that the increased fecundity is primarily related to an increased growth rate for white perch in lacustrine systems, and attainment of a greater size for mature females (Thoits 1958; Taub 1969).

The white perch does not contribute substantially to the commercial fishery of the Hudson River and has declined sharply from the 590 t (1.3 million lb) observed for the New York Bight region in the 1901 statistics (McHugh and Ginter 1978). Sheppard[9] reported that for the Hudson River the average catch between 1913 and 1964 was ~19,073 lb, ranging from 2,249 to 60,522 lb. The average commercial catch during 1965-74 was 1,600 lb.

However, the species has ecological importance in cycling nutrients within estuarine food webs and thus contributes to populations of commercially important marine and anadromous fisheries. The juvenile white perch in the Hudson River are prey for yearling and older striped bass, *Morone saxatilis*; adult white perch; and presumably other species such as the bluefish, *Pomatomus saltatrix* (Bigelow and Schroeder 1953; Texas Instruments Inc. footnote 7, 1976[10]).

The adaptability of the species to waters of different quality and chemical characteristics, and the high plasticity of fecundity and growth rate under various conditions (e.g., brackish waters vs. freshwater impoundments) suggest potential importance of white perch as highly suited to temperate zone aquaculture.

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IDENTIFYING CLIMATIC FACTORS INFLUENCING COMMERCIAL FISH AND SHELLFISH LANDINGS IN MARYLAND[1]

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ABSTRACT

In five of the seven most important commercial fisheries of Maryland an appreciable portion of the annual variations in catch can be linked with past fluctuations in the physical environment. The harvest figures were compared with appropriate annual characterizations of 40 years of daily environmental records using a variation of the stepwise multiple linear regression technique. The criterion for entry of a term into the regression was how well the given variable improved the prediction of a randomly chosen independent subset of catch figures. The identification of spurious predictor variables becomes less probable under this criterion. The results should help in the organization of further research and management concerning these species and may afford estimates of catches 1 or more years into the future.

Annual population levels of commercially harvested fish and shellfish usually fluctuate widely over the years. Such variation is often attributed to the influence of important environmental variables, such as water temperature, upon spawning success (Sissenwine 1978). Environmental variables may directly affect the mortality rates of prerecruits or indirectly exert influence by altering the abundance of forage or predators. Many other aspects of the ecosystem may also alter population levels (Cushing 1975); however, exact causative mechanisms in most fisheries are seldom known.

Year-to-year fluctuations in the abundance of exploited species will determine in part the magnitude of annual harvest of those species. But the relationship will not be completely deterministic, since landings will also be influenced by socioeconomic factors (e.g., prices and costs as they affect effort) as well as biological factors unrelated to exploitation (Ricker 1978). Despite these many complicating factors, significant correlations between various environmental variables and commercial landings of various species have been found in a number of fisheries. Dow (1977), for example, showed that temperature correlates well with the landings of 24 species of finfish, crustacea, and mollusks off the coast of Maine. Sutcliffe (1972) found freshwater input to St. Margaret's Bay to be a good indicator of fisheries production, possibly because of the stimulation of production caused by the nutrients in the runoff water. However, in neither case were the observed relationships demonstrated to help in predicting harvests, nor were the specific mechanisms responsible for the observed relationships rigorously delineated. In contrast, a regression model of brown shrimp landings off North Carolina, using temperature and salinity as independent variables, was found to be a reasonably accurate predictor of future landings (Hunt et al.[7]). Hunt's model has proven to be a useful management tool for this fishery, helping fishermen to decide how to gear up for the coming season.[8] Multiple linear regression has likewise been employed to explain variations in catch (e.g., Flowers and Saila 1972; Driver 1976). Only

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in the former instance, however, was there an attempt to validate the regression using independent data.

Thus, the value of correlative or regression models of fisheries is twofold: First, significant correlations can serve to guide research into identifying the causes of annual variation in catch; secondly, if validated, such models may forecast harvest in cases where more detailed deterministic models cannot be developed for lack of information.

The issue of model validation is especially important. Correlational models which best regress to the available data are often not the best predictors (Saila et al. 1980). In an effort to overcome this difficulty we have employed an amended version of stepwise regression analysis which does not rely solely on overall goodness-of-fit, but rather identifies those variables most likely to provide good predictions of data points not used in the actual regression.

To our knowledge multiple correlational models of the relationships between environmental variables and commercial landings in the Maryland portion of Chesapeake Bay have not been attempted in an algorithmic fashion. Because most of the dominant species reproduce in Maryland waters, the influence of environmental variation on harvest of these species may be particularly strong. Thus, we have developed multivariate regressions of the landings of major commercial species, using as predictors those environmental variables considered to have biological significance for the species being examined. Although measures of catch per unit effort (CPUE) would have been preferable as indicators of stock size, adequate effort data were not available. The results provide valuable insight into factors which may contribute to determining the population dynamics of these species and may also prove to be of value in establishing management practices.

SPECIES ADDRESSED AND DATA AVAILABLE

Seven dominant species in Maryland landings were selected for analysis. American oyster, *Crassostrea virginica*; blue crab, *Callinectes sapidus*; soft shell clam, *Mya arenaria*; and striped bass, *Morone saxatilis*, were chosen because they are the four species which yield the greatest dollar value to the Maryland economy. Menhaden, *Brevoortia tyrannus*, and alewife, *Alosa pseudoharengus* and *A. aestivalis* arbitrarily combined, were selected because they have been dominant in number of pounds harvested. The bluefish, *Pomatomus saltatrix*, was included because its harvest has increased dramatically in recent years, and there was interest in determining if this increase might be related to environmental variation.

A 33-yr record of annual catch data for 24 commercial species was available from records maintained by the Chesapeake Biological Laboratory and the NOAA Current Fisheries Statistics series. These records report the total Maryland landings (Chesapeake Bay and Atlantic Ocean) for each year. The Chesapeake Bay portion of the harvest heavily dominates the catches of the chosen species (85% or more of total). Because of the difficulty in obtaining sufficient information to separate Bay catch from the State total, the total was assumed to be representative of Chesapeake Bay.

ANNUAL CHARACTERIZATIONS OF ENVIRONMENTAL DATA

The environmental variables for which long-term records exist are water temperature, air temperature, salinity, and precipitation. All four have potential relevance to the levels of commercial harvest. Cross correlative relationships among these variables would be accounted for in the stepwise multivariate regression procedure employed in the analysis (discussed below). Daily recordings of these variables exist for a period exceeding 40 yr as taken from the Chesapeake Biological Laboratory pier at the mouth of the Patuxent estuary in Solomons, Md. Because this location is central to the Maryland portion of Chesapeake Bay, these data were assumed to be characteristics of conditions in the bay as a whole. Gaps in air temperature and precipitation from 1960 onwards were filled by data taken at the nearby Patuxent River Naval Air Test Center in Lexington Park, Md.

While catch figures represented the total landings for a season, environmental data existed with much finer temporal resolution. Our goal was to pair each annual catch figure with a value of an environmental property which might be representative of the effect that variable had on the stock during the year the daily readings were accumulated. One straightforward way of characterizing a year is to calculate the annual average of the variable in question. The stock,

however, may be more sensitive to shorter term deviations from this average. In an effort to quantify these deviations we devised four different ways of treating each of the original four time series to yield 26 annual series of environmental data.

The first of these methods, calculating the annual average, has already been mentioned. But the annual mean conveys little information on the cumulative amount of stress or benefit experienced by the populations because of the extreme high or low values of environmental variables. To portray the cumulative effects of these deviations, we defined variables analogous to the degree-days of agricultural science. Here the effect of a variable is assumed to be manifested only when its value goes beyond a certain "bias-level." If, for example, the organism is assumed to be cold stressed when the water temperature falls below 4°C, then 3 successive days of 1°C water temperature will contribute 9 degree-days towards the index of cold stress.

For each of the four variables recorded, a high and a low bias level were chosen so that when conditions exceeded these bounds at Solomons, we estimated that there were significant regions throughout the Maryland section of the Chesapeake Bay where fish and shellfish were probably stressed (or benefited) by the large excursions from the norm. These bias levels are shown in Table 1.

Of course, the fishery might be responding to individual episodes of stress, rather than the yearly cumulative value. We, therefore, elected to measure the lengths of the longest episodes during a year that a variable was beyond the bias values. These episodes were intermediate time-scale phenomena (on the order of 1 to several weeks), and we wished to avoid contamination from high frequency events. For example, salinity may have remained above 16.2 ppt for all of a 28 d period, save on the 15th day when it dropped to 16.1 ppt. To characterize the episode as 14 d in duration would clearly be erroneous. To avoid such contamination we chose a "gap-interval" for each variable ranging from 3 to 5 d. If the variable went beyond the bias level for a duration not exceeding the gap interval, the episode was not terminated, although the days on which the lapse occurred were not tallied in the episode length. Thus, the episode of high salinities mentioned above would be counted as 27 d.

TABLE 1.—Parameters used in calculating cumulative variables and episodes.

Variable	High bias	Low bias
Salinity	16.2 ‰	10.5 ‰
Water temperature	26.5°C	4°C
Air temperature	30°C	0°C
Precipitation	3 cm/d[1]	0 cm/d

[1]This value becomes 0.01 cm/d in calculating rain episodes, i.e., any day it rains is counted.

Finally, the possibility remains that the stocks might be acutely affected by short-term, intense stresses. We felt this eventuality would be reflected in the annual extremes of each variable.

These four operations, when applied to the four daily time series, yielded 26 annual time series of interest. (Cumulative and extreme low precipitations are uniformly zero by definition, and provide no information.) These series constituted the possible "predictor vectors" from which those yielding the best multiple regressions would be chosen. The values for the 26 variables calculated for the years 1938-76 are listed in Ulanowicz, Caplins, and Dunnington (1980).

REGRESSION METHODOLOGY

In most fish stocks, year class size is considered to be established by the juvenile stage (Cushing 1975). For example, oyster spat set (analogous to juvenile stages of finfish) is a good indicator of spawning success (Galtsoff 1964). Thus, recruitment (and subsequently harvest) is often correlated to those conditions in the past which helped determine the level of juvenile success. In populations where all individuals in a year class are recruited into the fishery at the same age, and annual landings consist primarily of a single year class, a significant correlation might be obtained when the environmental variable in question was lagged against landings by the number of years equivalent to the age at recruitment.

For most species harvested in Maryland, recruitment is not simultaneous for all members of a year class; landings in 1 yr may consist of members of several or many year classes. Thus, environmental characteristics important to establishing year class strength may be partially correlated with landings recorded over several years, and vice versa. In order to account for such extended partial recruitment, stepwise regressions were employed, allowing the contribution of a given environmental variable to be assessed by successively lagging that independent variable by annual increments so as to encompass the lifespan of most of the stock being fished, i.e.,

harvests are regressed against conditions during the same year, 1 yr ago, 2 yr ago, etc.

In the case of species which do not spawn in Maryland and where environmental conditions in the Chesapeake Bay would not influence year class size (i.e., menhaden and bluefish), any significant correlations arising would either be the result of how the Chesapeake Bay environmental conditions influence the availability of the species to Maryland fishermen, or how its conditions might be correlated with critical conditions at the remote spawning site. Oysters and striped bass, being the longer lived of the species of interest, were regressed against conditions as long ago as 9 yr in the past. Conditions affecting the remaining species were investigated over the past 5 yr.

As mentioned in the introduction, we wished to limit our attention to those variables which are most likely to be good predictors of future harvests. In conventional stepwise regression, that variable which increases the goodness-of-fit by the greatest amount (usually measured by R^2, the percentage of the variance explained by the model) is included as the next variable in the regression equation. We chose instead to enter that variable which improved the model prediction of independent data points by the greatest amount.

To implement this alternate criterion we randomly chose 25% of our data to be reserved for testing. At each step in the regression all of the remaining variables were entered in turn into a least squares multiple regression using the remaining 75% of the data (employing subroutine GLH from the Univac[9] STAT-PAK library). The coefficients derived for each entry were then used to see how well they would predict the test values of the dependent variable. That variable whose inclusion generated the greatest improvement in fitting the test data (as measured by the sum of the squares of the deviations) was entered into the prediction equation.

Ivakhnenko et al. (1979) suggested that one should continue to include terms until the prediction can no longer be improved. It became apparent during the first few runs, however, that with six or eight degrees of freedom in the test data, statistically insignificant improvements in predicting the independent data were occurring. Accordingly, no variable was added to the prediction equation when its F-to-enter statistic (calculated on the fit to the test data) dropped below 3.5. This somewhat low level of confidence (a little below 90%) was chosen so as not to exclude potential predictors early in the screening process. It should also be pointed out that because of the small number of points in the test data, a relatively large percentage of the error in the test data must be explained to meet this F-to-enter criterion (40-60% in our trials).

By separating test and regression data in a random manner, it was always possible that by chance the set of test data chosen for any single run was unduly influenced by high or low production years. Such bias in the test data could result in a predictor accurate only under particular circumstances. Hence, it was necessary to run several (and in the later stages of the screening process, many) trials with different randomly chosen sets of test data. Presumably, the predominance of any single sequence of predictor vectors among the various trials would be an indication that the associated model might be a robust tool for forecasting. Once the functional form of the best predictor has been chosen, the parameters of this equation are redetermined using the full data set.

The sequence of searches outlined above should provide a necessary (although not sufficient) test for prediction formulae.

RESULTS AND DISCUSSION

To facilitate easy recognition of the environmental variables in the regression equations that are to follow, we adopt a two-letter, one-digit code to designate each of the 260 possible predictor vectors. The first letter will be either A, C, E, or X according to whether the processed variable represented an annual average, cumulative deviation, episode, or extremum, respectively. The second letter will designate air temperature, water temperature, daily precipitation, or salinity by T, W, P, or S, respectively. When it is necessary to distinguish between high or low deviations of these variables, the low values will be designated by writing the second letter in the lower case. Finally, the digit will designate the number of years lag behind the harvest figures. As examples, Cs3 would indicate cumulative low salinity 3 yr in the past, whereas EW2 would denote the longest episode of high water temperatures 2 yr ago.

After the field of predictor variables for each fishery had been narrowed to five or fewer, 1,000

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

Monte Carlo trials were run for each species using different random combinations of test data. In five of the seven species considered, pairs of two variables were identified frequently enough to warrant their being cited as potential predictor formulae in Table 2. In one case (blue crab) no variables appeared often enough in the trials to warrant reporting a predictor equation. By contrast several sequences of oyster predictors appeared often, but no sequence predominated in the trials. About five separate sequences appeared with almost equal frequency. Hence, no formula for oysters is cited.

In the clam regression, Cw1 appeared as the primary predictor in over 50% of the trials. In roughly 20% of these instances CS2 was included as secondary predictor. No predictor was chosen 12% of the time. When the two selected variables were finally regressed against the entire data set, 60% of the total variance was explained, 49% by Cw1 alone. Environmental data were available to assess the predictive value of this equation for the year 1977. As can be seen in Figure 1, this projected value has a large deviation from the recorded measure, but this deviation falls within the range of errors in the hindcast.

Interpretation of this equation in terms of causality is complicated by the absence of effort data. For example, the effects of the rise in number of licensed clammers (from 3 in 1952 to 100 in 1957 to 200 in 1979 [Richkus et al.[10]]) on catch cannot be accounted for, and they may have been substantial. Still, the strong correlation between cumulative low water temperature lagged 1 yr and catch suggests a causal relationship.

[10]Richkus, W. A., J. K. Summers, T. T. Polgar, and A. F. Holland. 1980. A review and evaluation of fisheries stock management models. Martin Marietta Laboratories, Baltimore, Md., 177 p.

In Maryland, soft shell clams spawn in spring and fall (Pfitzenmeyer 1962). However, the spring set each year is almost totally eradicated because of predation by benthic feeding fish and crabs which migrate onto Maryland clam grounds each spring and leave each fall (Holland et al.[11]). Factors influencing the strength of the fall set (which occurs from October through December) and the ensuing survival of juveniles have not been identified. It appears that these factors are the ones most likely to have the greatest effect on the magnitude of commercial clam landings. Since Maryland is near the southern

[11]Holland, A. F., N. K. Mountford, M. Hiegel, D. Cargo, and J. A. Mihursky. 1979. Results of benthic studies at Calvert Cliffs. Final Report to Maryland Power Plant Siting Program. Ref. No. PPSP-MP-28, 229 p. Martin Marietta Laboratories, Baltimore, Md.

TABLE 2.—Potential predictors of landings (in metric tons) of designated species; see text for code to predictor variables.

Species	Regression	Multiple R^2	F	df
Soft clam, *Mya arenaria*	H_s = 372.4 + 13.56Cw1 + 3.765CS2	0.60	11.1	22
Menhaden, *Brevoortia tyrannus*	H_m = 888.4 + 45.99Ep5 − 9.126CT4	0.53	11.1	30
Bluefish, *Pomatomus saltatrix*	H_b = −48.20 + 1.948Ep5 + 0.1693Cs2	0.60	14.8	29
Alewives, *Alosa aestivalis* and *A. pseudoharengus*	H_a = 3,344 − 24.19Ep3 + 93.80Xt2	0.51	10.5	30
Striped bass, *Morone saxatilis*	H_r = 7,414 − 446.5AT3 + 2.435C11	0.45	8.3	30

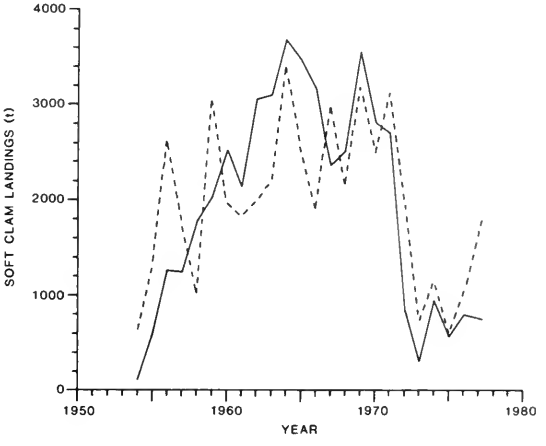

FIGURE 1.—Maryland soft clam landings in metric tons from 1952 to 1977 (solid line) and landings predicted using the regression model (dotted line) (Table 2). (Landings for 1977 did not enter into the derivation of the model.) Environmental factors were a cumulative low deviation in water temperature (with a 1-yr lag behind the harvest figure), and a cumulative high deviation in salinity (with a 2-yr time lag).

boundary of the geographical range of soft-shell clams (Manning[12]), cold water temperatures may, in some unexplained way, enhance the survival of a previous year's set.

Manning and Dunnington (1956) showed that Maryland clams grow at a rapid rate, achieving legal size (2 in, 5.1 cm) at an age of 16 to 22 mo. Hence clams spawned in the fall of one year would enter the commercial fishery during the spring 2 yr later. Extreme low water temperatures generally occur in January or February of each year and during some years coincide with periods of high salinities. Thus, both variables in the regression model could be exerting an effect on juvenile clams from set to the age of 6-7 mo, when they are approximately 0.5 cm (0.2 in) in size. Low water temperature may delay movement of predators into Maryland waters, permitting juvenile clams to grow to a less vulnerable size. High salinities during the juvenile life stages could also favor growth and rapid maturation of clams.

The remaining four regressions are composed of variables which are less readily explained. The two terms entering the menhaden regression have 4 and 5 yr lags (Table 2). But menhaden which make up Maryland landings are of ages 2 and 3, with almost no 4-yr-old fish taken (Merriner[13]). Thus, any causal mechanism suggested by the regression would have to be a second generation response, remembering that menhaden do not become sexually mature until ages 3 or 4. Ep5 appeared as the most important predictor in 37% of the trials with CT4 following as a secondary predictor in 23% of those cases. Menhaden catch is depicted in Figure 2.

Juvenile bluefish use Chesapeake Bay as a nursery area and there is the possibility that a distinct Chesapeake Bay stock of bluefish exists (Kendall and Walford 1979). Bluefish, being a marine species, are generally not found in low salinity waters, and their distributions can be well defined by salinity patterns (Lippson et al. 1980). Thus, the precipitation variable entering the regression (Table 2) may reflect diminished nursery habitat caused by high precipitation, resulting in a decline of harvestable fish in future

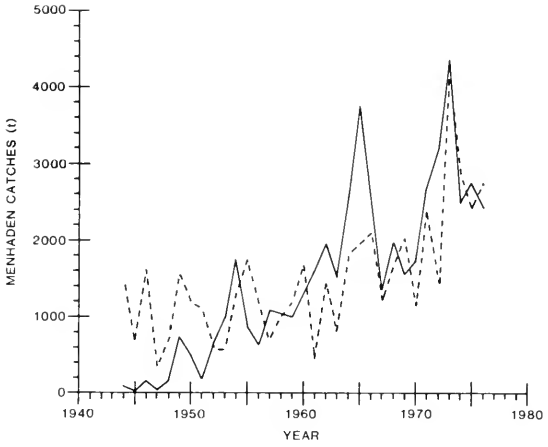

FIGURE 2.—Actual (solid line) and predicted (dotted line) catches in metric tons of menhaden, 1946-76, based on the regression model in Table 2. Environmental factors were an episode of low daily precipitation (with a 5-yr time lag behind the harvest figure), and cumulative high deviation in air temperature (4-yr time lag) which had a negative effect.

years. However, age composition of Maryland bluefish catch is unknown, and the particular lags in the regression are not readily explained. Bluefish harvests are illustrated in Figure 3. Ep5 appears as the primary predictor in 56% of the trials run with Cs2 following in 23% of those instances. It is noteworthy that the same variable (Ep5) appears as the most useful predictor of both menhaden and bluefish. Both species are coastal spawners, and it is entirely possible that

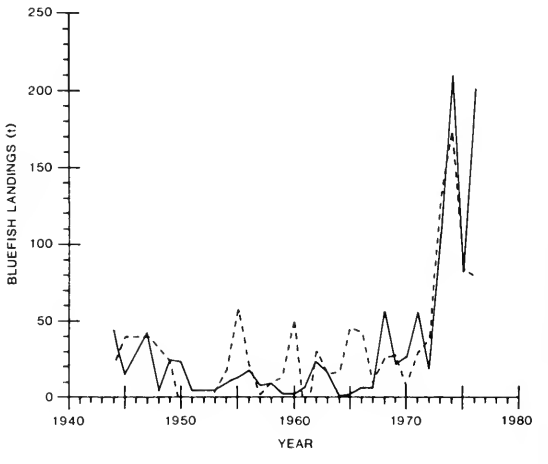

FIGURE 3.—Predicted (dotted line) and recorded (solid line) weights of bluefish landings in metric tons, 1947-76, based on the regression model in Table 2. An episode of low daily precipitation (5-yr time lag), and cumulative low deviation in salinity (2-yr time lag) were the environmental factors.

[12]Manning, J. H. 1957. The Maryland soft-shell clam industry. Study Report 2, 25 p. Maryland Department of Research and Education, Solomons, Md.

[13]J. V. Merriner, Chief, Division of Fisheries, Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516, pers. commun. September 1980.

the same causal mechanism is affecting the catches of both fishes.

Both species included in landings as alewives, *A. pseudoharengus* and *A. aestivalis*, are anadromous, tributary spawners in Maryland (Hildebrand and Schroeder 1927). Thus, poor spawning success could readily be related to low freshwater runoff caused by low precipitation. However, the age of first spawning of these species is from 3 to 5 yr, with the majority spawning at 4 or 5 (Davis et al.[14]). The regression (graphed in Fig. 4) suggests the possibility that recruitment in Maryland occurs at a younger age, but data on the age distribution of the catch are unavailable to confirm or refute this suggestion. The other variable entering the alewife regression (Table 2) is lagged by 2 yr. Since fish taken in a given year would have been present in the Atlantic Ocean 2 yr before being harvested, this correlation is difficult to explain in a causal manner. Ep3 is the major predictor in 50% of the trials and is followed by Xt2 in 20% of those cases.

The least significant of all the predictors cited is the one for striped bass (see Fig. 5). Both terms show a favorable correlation with cold air temperatures over a season. Cold seasons are

[14]Davis, J., J. V. Merriner, W. J. Hoagman, R. H. St. Pierre, and W. L. Wilson. 1971. Annual Progress Report, Anadromous Fish Project. Proj. No. Va. AFC7-1, 106 p. Virginia Institute of Marine Science, Gloucester Point, Va.

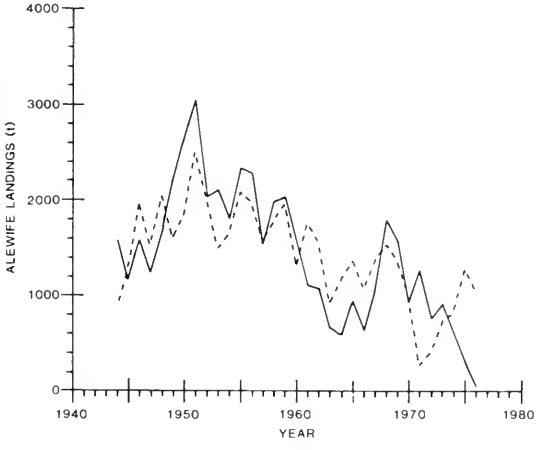

FIGURE 4.—Annual landings (solid line) in metric tons of alewife, 1944-76, as compared with predicted values (dotted line), based on the regression model in Table 2. Environmental factors were an episode of low daily precipitation (3-yr time lag) (negative effect) and an extremum of low air temperature (2-yr time lag).

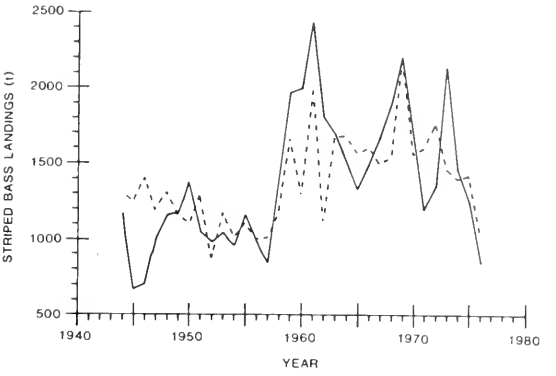

FIGURE 5.—Predicted (dotted line) and tabulated (solid line) landings in metric tons of striped bass from 1944 to 1976, based on the regression model in Table 2. Environmental factors were high annual average air temperature (3-yr time lag) (negative effect) and cumulative low air temperature (1-yr time lag).

conducive to greater amounts of ice formation along river edges. The scouring from ice floes contributes high quality detritus to the riverine system to supplement the food source for zooplankton, in turn providing the larvae with abundant food (Heinle et al. 1976). Boynton et al.[15] have previously remarked that year class success correlates jointly with cold winters and high runoff. The chosen variables did not dominate the trials heavily. AT3 was the major predictor in only 33% of the trials, one-third of which were accompanied by the variable Ct1. Xs4 appeared as the major predictor almost as often (25% of the time there was no major predictor), but did not result in a significant correlation with the full data.

An examination of the power spectra of the errors of the five models (using subroutine POWDEN in Univac STAT-PAK) revealed no appreciable differences from the spectral pattern of random noise.

CONCLUDING REMARKS

Perhaps the most significant observations to be made from this exercise involve the comparison of the results reported herein with those reported previously from a conventional search for

[15]Boynton, W. R., E. M. Setzler, K. V. Wood, H. H. Zion, M. Homer, and J. A. Mihursky. 1976. Potomac River fisheries program ichthyoplankton and juvenile investigations. Ref. No. 77-169CBL, 328 p. Center for Environmental and Estuarine Studies, Solomons, Md.

predictors using the same data (Ulanowicz, Ali, and Richkus 1980). The major predictors cited in the previous work were either identical to, or qualitatively similar to, the initial variables selected by the more usual analysis. In that earlier work up to seven terms appeared in one regression equation (F-to-enter criterion of 4.0), and R^2 values ranged as high as 0.86 with four variables. Despite having dropped the F-to-enter criterion below the 90% confidence level, the joint criterion that the variables chosen also be reasonably good "internal predictors" appears to have resulted in a more stringent combined test for selecting variables. Fewer spurious predictors are likely to appear using the new criteria. Although the regression with the full set of data will not be as tight as might otherwise be possible, there is less likelihood that predictions on independent data will be wildly in error. In the words of Ivakhnenko et al. (1979), the "fan of predictions" has been narrowed.

When the number of possible predictor vectors is large compared with the number of observations (as it is in this study), there is concern that multiple regression R^2 values can be inflated (Rencher and Pun 1980). Fortunately, the method described herein does not rely on R^2 values alone. Before a variable is chosen for further consideration, it must explain a significant fraction of the variance in several randomly assembled groups of test data. To see how well this might screen against including spurious variables, the search procedure for the menhaden predictor was rerun with the yearly observations randomly scrambled. Out of 28 possible trials with the original data, at least one variable was added in exactly half the trials (with an average F-to-enter of 9). In all but 2 of those 14 successes the first variable entered was identical (Ep). By contrast, only 5 successful trials were recorded with the scrambled data (average F-to-enter was 5), although one variable did appear in 3 of those successful trials. Nonetheless, there is an evident decrease in the frequency and number of variables with successful F-to-enter ratios in the trials with scrambled data. The only species studied giving results nearly as poor as the scrambled data was blue crab, and those findings were disregarded.

Unfortunately, the results of the present analysis must still be viewed with caution. Although the possibility of identifying a spurious correlation as a predictor has been decreased, it cannot be totally eliminated. The fact that substantial portions of the variability in landings of all the species considered can be explained by a few environmental variables suggests the important role which environmental conditions play in determining stock size. However, our inability to interpret many of these relatinships in a causal manner reflects both a lack of knowledge of mechanisms influencing fish population dynamics as well as an unfamiliarity with the auto and cross correlative relationships between the variables introduced into the regression process. (Because the procedure employed was stepwise, true causal variables may have been displaced in the regressions by spurious variables which by chance were closely correlated. No detailed analysis of the independent variable data sets was performed to address this issue. More analyses would be required to fully account for this possibility.)

Despite these limitations, the analyses appear to have been fruitful, particularly in the case of the soft clam. As for the other species, the value of the models will be determined when sufficient data are available to assess their predictive value for future landings. Only then can it be ascertained whether any chosen predictor was spurious or reflected some unknown causal relationship between environmental variation and stock dynamics. Meanwhile, the terms appearing in the regressions may engender new research projects into the mechanisms determining the sizes of these important fisheries stocks.

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AERIAL SURVEYS FOR MANATEES AND DOLPHINS IN WESTERN PENINSULAR FLORIDA

A. Blair Irvine,[1] John E. Caffin,[2] and Howard I. Kochman[1]

ABSTRACT

Low altitude aerial surveys were conducted to count West Indian manatees, *Trichechus manatus*, and bottlenose dolphins, *Tursiops truncatus*, in western peninsular Florida. A total of 554 manatees was observed in 297 groups. Most of the manatees (58.5%) were sighted in the Collier-Monroe Counties in shallow, brackish inshore areas. A total of 1,383 bottlenose dolphins was observed in 431 herds, including 700 (in 146 herds) in the Gulf of Mexico, 491 (in 185 herds) in bays, and 192 (in 100 herds) in marsh-river habitats.

West Indian manatees, *Trichechus manatus*, and bottlenose dolphins, *Tursiops truncatus*, occur in rivers, estuaries, and coastal areas in Florida (Moore 1953; Layne 1965; Hartman 1974[3]; Irvine and Campbell 1978). Manatees are dispersed throughout Florida waters during the summer, but concentrate around warmwater sources in winter (Hartman footnote 3; Irvine and Campbell 1978). Aerial surveys indicate that bottlenose dolphins are also well dispersed in coastal waters of Florida (Odell 1976, 1979; Leatherwood 1979; Odell and Reynolds 1980[4]). However, localized distribution patterns and seasonal changes in distribution and abundance have only been documented in a few areas for manatees (Odell 1976, 1979; Irvine et al. 1978[5]; Shane 1980[6]) or dolphins (Odell 1976, 1979; Shane and Schmidly 1978[7]; Irvine et al. 1979[8]). The distribution of manatees and dolphins in various habitat types and salinities in Florida also is unclear.

More information is needed to serve as a basis for sound conservation and management decisions because manatees and dolphins are protected by the Marine Mammal Protection Act of 1972; manatees are also protected by the Endangered Species Act of 1973. Southwestern Florida, encompassing Everglades National Park (ENP; Monroe County) and the Ten Thousand Islands (Collier-Monroe Counties), is of particular interest because this area has been relatively unaffected by human development. Abundance, habitat use, and herd size information is therefore of interest for comparison with more developed areas.

We conducted a series of aerial surveys from July to December 1979 to examine the distribution and relative abundance of manatees and dolphins from Bayport, Hernando County (lat. 28°32′N, long. 82°39′W), Fla., south to Flamingo Ranger Station (ENP), Monroe County (lat. 25°08′N, long. 81°02′W), Fla.

METHODS

Surveys were conducted during five periods: 24 through 29 July, 6 through 11 and the 17th of

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[2]Denver Wildlife Research Center, Gainesville Field Station, Gainesville, Fla.; present address: U.S. Forest Service, P.O. Box A.D., Umilla, FL 32702.

[3]Hartman, D. S. 1974. Distribution, status, and conservation of the manatee in the United States. Report to U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, Wash., D.C. National Technical Information Service PB 81 140725.

[4]Odell, D. K., and J. R. Reynolds III. 1980. Distribution and abundance of the bottlenose dolphin, *Tursiops truncatus*, on the west coast of Florida. Report to the U.S. Marine Mammal Commission, Wash., D. C. National Technical Information Service PB 80-197650.

[5]Irvine, A. B., M. D. Scott, and S. H. Shane. 1978. A study of the West Indian manatee, *Trichechus manatus*, in the Banana River and associated waters, Brevard County, Florida. U.S. Fish and Wildlife Service, National Fish and Wildlife Laboratory, Final Draft Contract Report to John F. Kennedy Space Center, NASA, Kennedy Space Center, FL 33899. Contract No. CC 63426A, KSC-DF-112.

[6]Shane, S. H. 1980. Manatees (*Trichechus manatus*) in Brevard County, Florida: Abundance, distribution and use of power plant effluents. Report to Florida Power and Light Co., P.O. Box 13100, Miami, FL 33101. Contract No. 61552-86540.

[7]Shane, S. H., and D. J. Schmidly. 1978. The population biology of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, in the Aransas Pass area of Texas. Report to U.S. Marine Mammal Commission, Wash., D.C. National Technical Information Service PB 283-393.

[8]Irvine, A. B., M. D. Scott, R. S. Wells, J. H. Kaufmann, and W. E. Evans. 1979. A study of the movements and activities of the Atlantic bottlenosed dolphin, *Tursiops truncatus*, in-

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621-630

September, 2 through 8 October, 2 through 8 November, and 3 through 9 December 1979. Weather permitting, surveys were conducted on consecutive days in a chartered Cessna[9] 172 aircraft at an airspeed of about 160 km/h and an altitude of about 150 m. The final day of the September survey was postponed until 17 September because of adverse weather caused by Hurricane Frederic. The flight on 6 December was shortened, and flights scheduled for 7 and 8 December were cancelled due to inclement weather. The cancellation of those flights prevented December coverage of Charlotte Harbor and associated rivers, all of the Caloosahatchee and Orange Rivers, and the area from Estero Bay (Lee County) south to the Broad River (Monroe County) in ENP. The Whitewater Bay area of ENP was surveyed on 9 December 1979. After the July surveys, an extra survey day was added to the schedule, and daily coverage was redistributed to shorten flights in south Florida. Daily surveys lasted from 2 h 25 min to 6 h 21 min ($\bar{x}$ = 3 h 52 min).

Flights usually began between 0730 and 0800 h. The right door of the aircraft was removed to increase visibility on the 7 September flight and on all flights in subsequent months. One observer was seated in the right front and another in the left rear. Sighting locations of all manatees and dolphins were noted on charts of each earea by the forward observer. Comments were dictated into a cassette tape recorder, or noted directly on the chart. Calves were defined as small manatees or dolphins closely associating with larger animals of approximately twice their size (after Irvine and Campbell 1978). Dolphins or manatees within an arbitrary distance of about 100 m of conspecifics were counted as being in the same "herd" or group. Use of the term "herd" to describe social aggregations of dolphins is well established in the literature by Norris and Dohl (1980), but "herds" of manatees are not known to occur (Hartman 1979; Reynolds 1981).

Flight routes were marked on maps of the entire western Florida study area to facilitate consistent coverage on successive surveys. The routes were selected to cover probable manatee habitat (Hartman footnote 3; Irvine and Campbell 1978). Survey routes generally followed the 2 m bottom contour. The deepwater shipping channel was also surveyed in Tampa Bay. Pilots used the route maps to navigate, leaving the observers free to scan for animals. The plane deviated from the route only to investigate sightings and to count or photograph animals.

Areas surveyed included 1) bays and estuaries; 2) the Caloosahatchee River to the Ortona Lock in July and to Moore Haven on other surveys; 3) canals, bayous, rivers, and creeks (>1 m deep) up to 25 km inland; 4) the Intracoastal Waterway (ICW); 5) coastal areas to 0.5 km offshore, or to depths of about 2 m where shoals extended well offshore (Pasco and Hernando Counties).

Sighting locations on the flight record charts were categorized into three habitat types: 1) offshore: the Gulf of Mexico, 2) bay-estuary: bays, estuaries, and large rivers with direct access to the Gulf of Mexico, and 3) marsh-river: complex marsh habitats (Leatherwood and Platter[10]), inland bays (Monroe County), and narrow rivers. Using criteria from Remane and Schlieper (1971), salinity at each sighting location was subsequently classified as fresh (<0.5‰ salt), brackish (0.5 to 30‰ salt), or marine (>30‰ salt) based on available reports (E.P.A.[11]; Wang and Raney 1979[12]; U.S. Department of Commerce 1973; Weinstein et al. 1977; Schmidt and Davis 1978[13]). Offshore habitats were always categorized as marine, even though salinities in some areas might have been influenced by tide and freshwater runoff from recent storms. Relative survey effort was estimated as the percentage of total flight time in each habitat and salinity type.

Patterns of relative abundance and mean herd or group size were evaluated using chi-square and analysis of variance (ANOVA) procedures (Sokal and Rohlf 1969). Multiple comparisons among means were analyzed with Duncan's

cluding an evaluation of tagging techniques. Report to U.S. Marine Mammal Commission, Wash., D. C. National Technical Information Service PB 298 042.

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

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Multiple Range Test (Steel and Torrie 1960). A square root transformation ($\sqrt{\text{herdsize} + 0.5}$) was applied to the counts to make them suitable for parametric analysis (Steel and Torrie 1960). Computations were performed with programs of the Statistical Analysis System (Helwig and Council 1979) at the University of Florida, Gainesville, Fla.

RESULTS

Manatees

Two hundred and ninety-seven groups of manatees, totaling 554 individuals, were observed during 121.8 survey hours (Fig. 1). Numbers sighted (Table 1) and average number of individuals per groups (Table 2) varied by county and month. Total numbers of manatees sighted increased from September to November, but the total per county consistently increased only in Monroe County. Total counts were not statistically compared among counties because habitat type, weather, and amount of survey area were not equivalent.

Ninety-four percent of the groups sighted consisted of one to four animals (Fig. 2). Group sizes were not observed with equal frequency, and more than half of the 297 sightings were of single animals ($P<0.005$; chi-square). However, 367 (66.2%) of the 554 manatees sighted were in groups. Pooled samples of all counties indicated that group size-frequency distributions did not vary significantly between months ($P>0.80$; chi-square).

Mean group size for the pooled sample of all sightings was 1.9 (SE = 0.12). A subset of data, including only those counties with sightings in each month (Monroe, Lee, and Sarasota Counties), was analyzed as a two-way ANOVA. This analysis provided no evidence of a month by county interaction ($P>0.85$), indicating that any pattern of monthly variation in group size was comparable for those three counties. Monthly variation in average group size, analyzed as a separate one-way ANOVA for each county, was significant ($P<0.05$) only in Hillsborough County, due to high December counts at warmwater effluents.

Numbers of manatees sighted were not proportional to the amount of survey time in each habitat type or salinity ($P<0.005$; chi-square). Pooled samples from all counties indicated that numbers of manatees sighted per month varied significantly by salinity and habitat ($P<0.0005$; chi-square). Except in December, substantially more manatees were sighted in marsh-river habitats than in other habitat types, and most were in brackish water (Table 3).

From 51 to 100 manatees, representing 54.3 to 75.7% of those sighted on July to November surveys and 58.5% overall, were observed in Monroe and Collier Counties (Table 1). Manatees were consistently sighted in Whitewater Bay, Chevalier Bay, and in the Lopez River (ENP, Monroe County), but the largest concentrations were found in Collier County from Marco Island to Chokoloskee. Manatees may have been overlooked if they were not near the surface or creating surface wakes or mud trails because of water turbidity (estimated visibility 0-0.5 m).

A maximum of two manatees per survey was sighted in Charlotte Harbor (Charlotte County; Fig. 1) and small numbers of manatees were consistently sighted in Pine Island Sound, Matlacha Pass, San Carlos Bay, in the lower reaches of the

TABLE 1.—Numbers of manatees and bottlenose dolphins observed, by county, during aerial surveys in western peninsular Florida from July to December 1979. C = calves.

	Manatees					Bottlenose dolphins				
County	July	Sept.	Oct.	Nov.	Dec.	July	Sept.	Oct	Nov.	Dec.
Charlotte	4	5	6	0	[1]1	13+1C	22+1C	11+1C	1	[1]12+2C
Collier	41	49+2C	63+1C	49	([2])	9	20	11	29+1C	([2])
De Soto	0	0	0	0	([2])	0	0	0	0	([2])
Glades	0	0	0	1	([2])	0	0	0	0	([2])
Hendry	0	0	0	2+2C	([2])	0	0	0	0	([2])
Hernando	0	0	0	0	0	4	0	7	8	0
Hillsborough	16	3	0	0	47+3C	30+2C	17+2C	17	0	3
Lee	15	17+1C	7	26+1C	[1]12	34	37+1C	100+1C	32	[1]62+3C
Manatee	6	0	3	4	0	8+2C	6	44+3C	13	44+1C
Monroe	9+1C	10	20	48+3C	[1]28	15	35+2C	26+1C	66	[1]28+4C
Pasco	0	0	0	0	1	2	17+1C	27	119+3C	59+3C
Pinellas	0	0	0	0	7	56+1C	36+3C	39	73+2C	33+1C
Sarasota	2	6	11	14+1C	6	12+1C	60+4C	23+1C	6	9
Total	93+1C	90+3C	110+1C	144+7C	102+3C	183+7C	250+14C	305+7C	347+6C	250+14C

[1]Incomplete survey
[2]Not surveyed

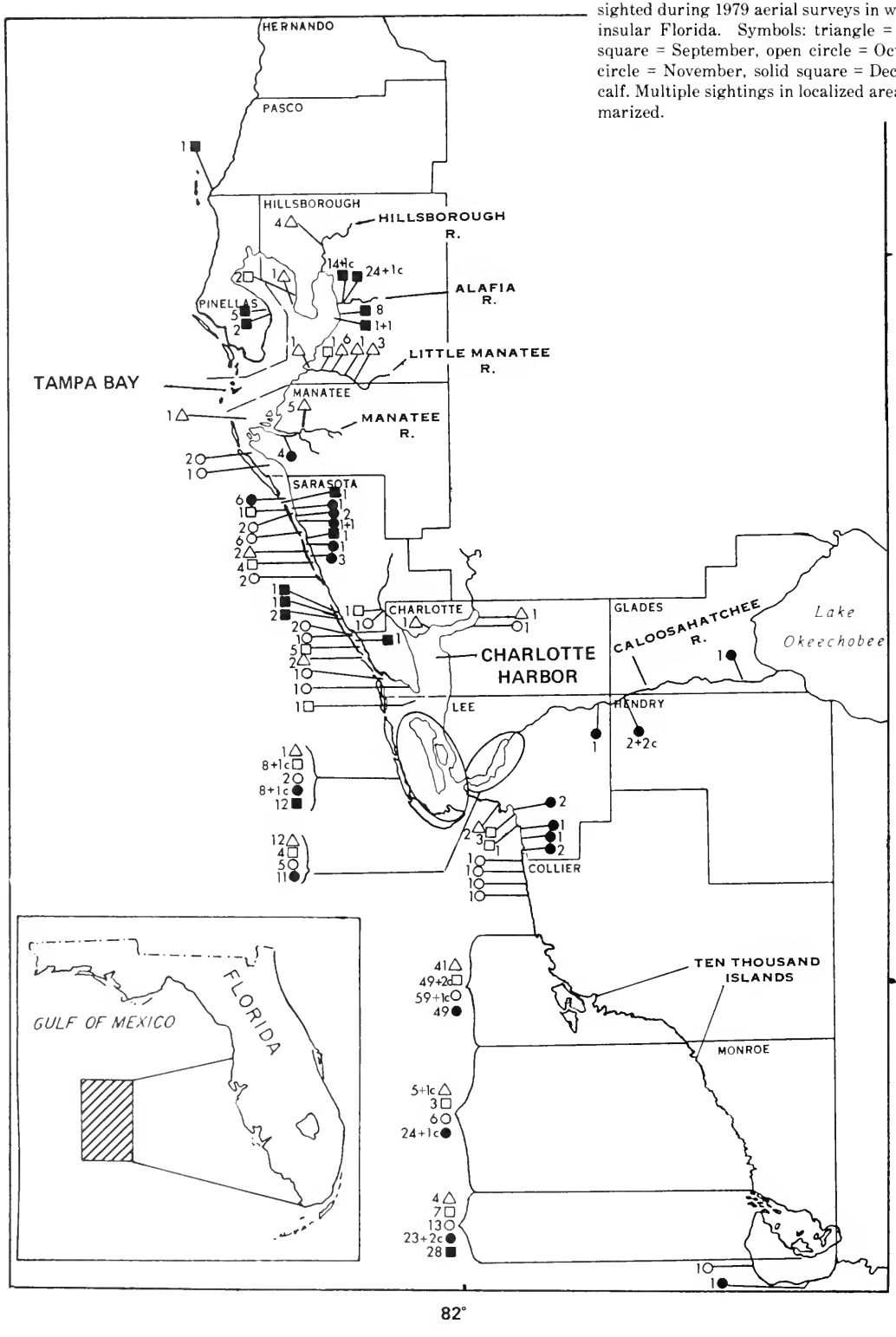

FIGURE 1.—Locations and numbers of manatees sighted during 1979 aerial surveys in western peninsular Florida. Symbols: triangle = July, open square = September, open circle = October, solid circle = November, solid square = December, c = calf. Multiple sightings in localized areas are summarized.

TABLE 2.—Average group or herd size of manatees and bottlenose dolphins sighted, by county, during aerial surveys of western peninsular Florida from July to December 1979.

	Manatees						Bottlenose dolphins					
County	July	Sept.	Oct.	Nov.	Dec.	Composite average	July	Sept.	Oct	Nov	Dec.	Composite average
Charlotte	1.3 (0.33;3)	5.0 (--;1)	1.2 (0.20;5)	—([2])	1.0 (--;1)	1.6 (0.4,10)	2.8 (0.86,5)	1.9 (0.40;12)	1.7 (0.57;7)	1.0 (--;1)	3.5 (1.50;4)	2.2 (0.33;29)
Collier	1.7 (0.27,24)	2.0 (0.38;25)	1.5 (0.16;42)	1.5 (0.15;33)	([3])	1.7 (0.11;12)	2.3 (0.63;4)	1.5 (0.33;13)	1.4 (0.26;8)	2.7 (0.84,11)	([3])	1.9 (0.30;36)
De Soto	—	—	—	—	([3])		—	—	—	—	([3])	—
Glades	—	—	—	1.0 (--;1)	([3])	1.0 (--;1)	—	—	—	—	([3])	—
Hendry	—	—	—	4.0 (--,1)	([3])	4.0 (--;1)	—	—	—	—	([3])	—
Hernando	—	—	—	—	—	—	4.0 (--;1)	—	7.0 (--;1)	1.3 (0 21;6)	—	2 4 (0.75;8)
Hillsborough	2.7 (0.84,6)	1.5 (0.50;2)	—	—	12.5 (4 94,4)	5.8 (2.11;12)	4.0 (0.57;8)	2.7 (1.13,7)	3.4 (2.40;5)	—	1.5 (0.50,2)	3.2 (0 66;22)
Lee	1.9 (0.30;8)	1.6 (0.24;11)	2.3 (0.88;3)	1.9 (0.32;14)	1.5 (0.19,8)	1.8 (0.14;44)	3.1 (0 68,11)	1.7 (0.24;22)	2.5 (0.36;41)	1.9 (0 41;17)	5.4 (1.45;12)	2 6 (0.27,103)
Manatee	3.0 (2.00;2)	—	1.5 (0.50;2)	4.0 (--;1)		2.6 (0.81;5)	3.3 (1.45;3)	1.5 (0.29;4)	4.7 (1.74,10)	2 6 (0 98;5)	15 0 (8.14,3)	4 8 (1 34,25)
Monroe	1.3 (0.16;8)	1.1 (0.11;9)	1.7 (0.36,12)	1.7 (0.26;31)	1 6 (0.34,18)	1.5 (0 14;78)	1.7 (0.33,9)	2.0 (0.58;19)	1.5 (0.15;18)	1.9 (0.22;35)	2.1 (0.65;15)	1.9 (0 18,96)
Pasco	—	—	—	—	1.0 (--;1)	1.0 (--,1)	2.0 (--;1)	4 5 (3.50;4)	27.0 (--;1)	20.3 (10.72;6)	10.3 (6.74;6)	12.8 (4 40;18)
Pinellas	—	—	—	—	3.5 (1.50;2)	3.5 (1.5;2)	2.7 (0.49;21)	4 3 (1 24;9)	3.9 (1.29,10)	5.0 (1 76;15)	4.3 (1.56,8)	3.9 (0.55;63)
Sarasota	2.0 (--;1)	2.0 (1.00;3)	2.8 (1.11;4)	2.5 (0 76;6)	1.2 (0.20;5)	2.1 (0.37,19)	2.2 (0.31,6)	5.8 (2.40;11)	4 8 (2.33;5)	1 2 (0.20;5)	2.3 (0.63,4)	3.7 (0.96;31)

[1]Standard error of the mean and *n* (sightings) in parentheses; -- = no value.
[2]No sightings.
[3]Not surveyed.

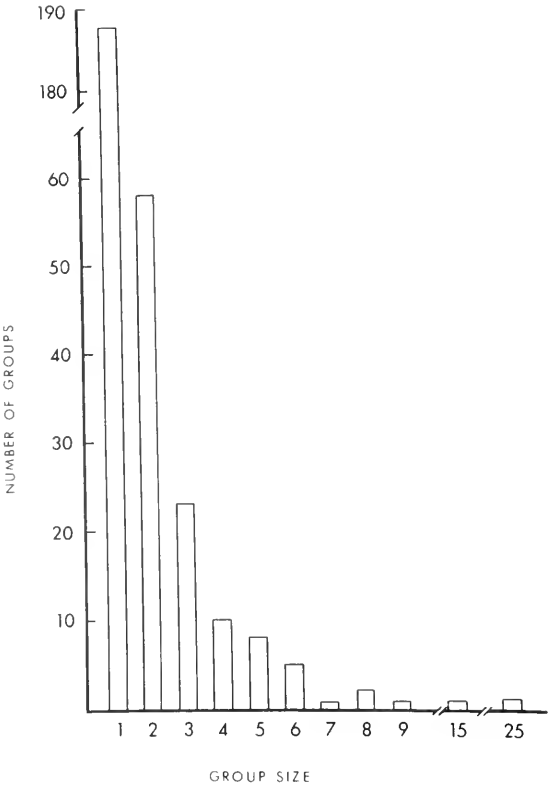

FIGURE 2.—Group size-frequency distribution of manatees sighted during aerial surveys from July through December 1979.

Caloosahatchee River, and in Estero Bay (Lee County). Manatees were sighted in the Upper Caloosahatchee River (Glades and Hendry Counties) only in November. Manatees were not sighted near the warmwater refuge in the Orange River, Lee County (Hartman footnote 3), but the area was not surveyed in December when ambient air and water temperatures were coldest.

A few manatees were consistently sighted between Charlotte Harbor and Tampa Bay. The animals were sighted in Lemon Bay, Roberts Bay, and Little Sarasota Bay, and were often near the channel of the ICW.

North of Sarasota County, manatees were primarily sighted in rivers emptying into Tampa Bay, including the Hillsborough, Alafia, Manatee, and Little Manatee Rivers. Our observations in Hillsborough and Manatee Counties may have been hampered in September by cloud cover and in October by turbid waters resulting from recent flooding.

Manatees were observed near warmwater refuges described by Hartman (footnote 3) only during the December flights. A total of 40 manatees was sighted at the two warm effluents of the Gibsonton Phosphate Plant in the Alfia River (Hillsborough County). Eight manatees were sighted in the Big Bend Power Plant effluent (Hillsborough County), and a cow and calf were observed just offshore of the effluent. Five manatees were observed at the P. L. Bartow Plant effluent (Pinellas County), and two manatees were observed near the intake canal. A single manatee was sighted in the intake canal of the Anclote Power Plant (Pasco County).

A maximum of three calves per county was sighted on any survey. Total percentage of calves sighted ranged from 0.9 to 4.9% on different surveys.

Bottlenose Dolphins

Four hundred and thirty-one herds, totaling 1,383 bottlenose dolphins, were observed. The total number of dolphins sighted increased from July to November, but fluctuated in most counties with no obvious trends (Table 1). Sightings were common in interior bays and rivers in ENP

TABLE 3.—Manatee and bottlenose dolphin sightings in different habitat-types and estimated salinities.

	Manatees						Bottlenose dolphins					
	Habitat-type			Salinity			Habitat-type			Salinity		
	Off-shore	Bay-estuary	Marsh-river	Fresh (<0.5‰)	Brackish (0.5-30‰)	Salt (>30‰)	Off-shore	Bay-estuary	Marsh-river	Fresh (<0.5‰)	Brackish (0.5-30‰)	Salt (>30‰)
Mean group or herd size (±SE)	1.29 (0.13)	2.38 (0.34)	1.69 (0.10)	1.93 (0.35)	1.85 (0.14)	1.93 (0.21)	4.79 (0.70)	2.65 (0.19)	1.92 (0.19)	0	2.19 (0.14)	3.97 (0.44)
No. of groups or herds	14	85	198	14	240	43	146	185	100	0	184	247
No. of animals (percent)	18 (3.2)	202 (36.5)	334 (60.3)	27 (4.9)	444 (80.1)	83 (15.0)	700 (50.7)	491 (35.5)	192 (13.9)	0	403 (29.1)	980 (70.9)
Percent of survey time	17.7	44.3	38.0	8.9	50.1	41.0	17.7	44.3	38.0	8.9	50.1	41.0

and well into Tampa Bay. In the Charlotte-Lee Counties area, dolphins were common in the Gulf of Mexico, around Pine Island, and occasionally in the lower Caloosahatchee River. Most coastal sightings were within 0.5 km of the beach.

Dolphin herd sizes were not sighted with equal frequency (Fig. 3); most sightings (56%) consisted of two or more animals ($P<0.005$; chi-square). Mean herd size for the pooled sample of all sightings was 3.2 dolphins/herd (SE = ±0.26). Effects of county and month on average herd size in counties with sightings in each month (Table 2) were analyzed as a two-way ANOVA. The county by month interaction was significant ($P<0.0005$), indicating that monthly variations in dolphin herd sizes were not comparable among counties. A separate one-way ANOVA for each county indicated that monthly variation in herd size was significant ($P<0.05$) only in Lee County, due to a high December mean. Pooled sightings from all counties indicated that herd size-frequency distributions varied significantly between months ($P<0.001$; chi-square), with fewer single dolphins and more large groups (>4) sighted in July and December.

Numbers of dolphins observed were not proportional to the amount of survey time in different habitats and salinities ($P<0.005$; chi-square). More animals were observed off the beach and in saltwater (Table 3), but monthly trends were not apparent. Dolphins were not sighted in freshwater. Pooled samples from all counties where sightings occurred indicated that numbers of dolphins sighted per month varied significantly by habitat and salinity ($P<0.001$). Most dolphins were sighted offshore in Pinellas and Sarasota Counties; more animals were in bay-estuary than in other habitats in Lee County; and most were in marsh-river habitats in Collier and Monroe Counties.

A maximum of 5.3% calves was observed during both the September and December surveys. A high of 12.5% calves was sighted in Monroe County in December, but this total may not be representative because relatively few dolphins were sighted in the area during the abbreviated surveys (Table 1).

DISCUSSION

Manatees are usually sighted in small groups when away from warmwater refuges. Eighty-six percent of the sightings during aerial surveys by Odell (1979) and 89% of the sightings by Hartman (1979) were of one to four manatees. Our results and those from other surveys (Hartman 1979; Odell 1979; Reynolds 1981) indicate that the greater percentage of manatees sighted are found in groups, but one is the most common group size. Although Hartman (1979) suggested that manatees are "essentially solitary," solitary manatees are nevertheless a minority of the total numbers sighted.

Odell (1979) sighted from 0 to 71 manatees

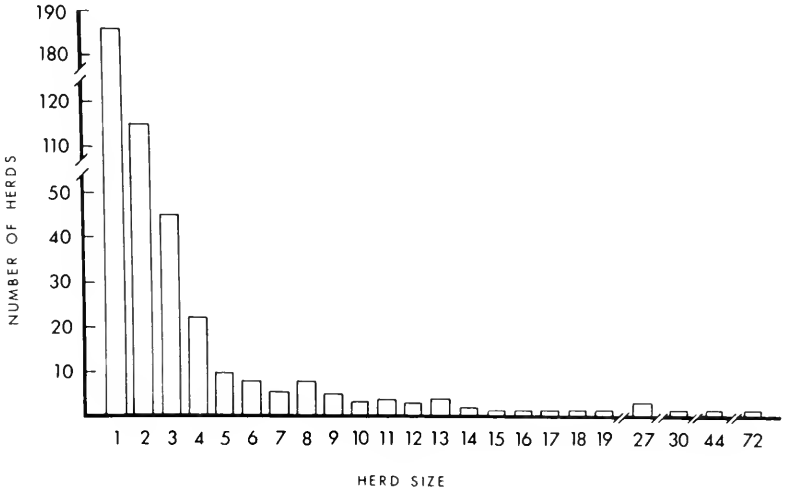

FIGURE 3.—Herd size-frequency distribution of bottlenose dolphins sighted during aerial surveys from July through December 1979.

during transect surveys conducted from July to December 1973 through 1976 in Monroe and Collier Counties. Hartman (footnote 3) sighted 45 manatees in Monroe and Collier Counties during a summer survey; Irvine and Campbell (1978) reported observing 163 manatees during a 1976 winter survey of the same area. Although abundance reports by different authors are not completely comparable because of variability among survey methodologies, results of our study clearly support previous reports that southwestern Florida is a center of manatee abundance (Moore 1951; Hartman footnote 3; Irvine and Campbell 1978).

Southerly shifts in the distribution of manatees in Florida during the fall were predicted by Moore (1951) and Hartman (footnote 3). Although total counts in Monroe and Collier Counties generally increased during fall surveys, the significance of this trend is unclear. Increased sightings may correlate with changes in manatee abundance, but could also indicate that the animals are for some reason more easily observed in that season. In any event, a southerly autumn shift in distribution cannot be conclusively shown based on our data.

The preponderance of manatee sightings in brackish water and marsh-river habitats occurred in the areas of Collier and Monroe Counties, which are characterized by that combination of habitat and salinity. Inland bays in ENP and Ten Thousand Islands area of Collier County were classified as "marsh-river" habitat because access to the Gulf of Mexico is restricted by relatively narrow or shallow channels. Although the survey results may be general indicators of habitat use, they should be viewed with some caution because all habitat types were not surveyed equally, and local salinities may have varied seasonally due to runoff from rainfall. Irvine and Campbell (1978) reported the relative frequencies of manatee sightings in fresh, brackish, and salt water as 19.1, 42.5, and 38.3%, respectively, during winter surveys, and 35.2, 34.9, and 29.6% during a summer survey of the entire state. In contrast, 80% of the manatees sighted in our surveys were in brackish water (Table 3).

The few sightings in Charlotte Harbor are noteworthy because manatees are often sighted by residents in this area (Moore 1951; Hartman footnote 3), and 36 manatees were counted in Charlotte Harbor during a summer aerial survey by Hartman (footnote 3). Manatee use of the Bartow and Anclote power plants has not been specifically reported, but two sightings mapped by Irvine and Campbell (1978) were at these plants.

We sighted few manatee calves (4.9% maximum per survey) compared with other surveys. Calves made up 5.2% of the animals sighted by Odell (1979) in Collier and Monroe Counties in 1973 through 1976, but during a 1976 winter survey of the same area, 10.4% of the manatees sighted were calves (Irvine and Campbell 1978). Leatherwood (1979) counted 9.9% calves in the Indian and Banana Rivers in eastern Florida, and Irvine and Campbell (1978) reported overall calf percentages of 9.6% in winter and 13.4% in summer from surveys of the entire state. Odell (1979) suggested that the tendency of calves to stay close to their mothers might result in fewer calf sightings in turbid waters, but this hypothesis has not been verified. Too few calves were sighted in our study to indicate seasonal reproductive trends.

The dolphin sightings are of particular interest due to the paucity of information on *T. truncatus* in nearshore areas of western peninsular Florida. The sightings were not analyzed for abundance and density estimates (see discussion by Leatherwood et al. 1978), because flight routes were designed to optimize manatee sightings and were not flown as straight lines. Our observations can, however, provide information on dolphin herd size and habitat use.

Average herd size (3.2 dolphins/herd) was considerably smaller than herd sizes reported from other aerial surveys in nearshore areas. In coastal waters of Alabama, Mississippi, and Louisiana, herd sizes averaged 25.2 dolphins with herd size in marshlands averaging 16.7 (Leatherwood and Platter footnote 10). Subgroups contained a mean of 5 dolphins in sounds and 3.8 dolphins in marshes (Leatherwood and Platter footnote 10). Barham et al. (1980) reported that herd sizes averaged 6.95 dolphins in Texas, and Leatherwood (1979) reported herds averaging 8.20 dolphins in eastern Florida. In primarily estuarine areas of western Florida, group size (equivalent to herd size as used here) was 4.8 dolphins/group (Irvine et al. 1981). Differences between observed herd sizes have been attributed to the influence of geography and habitat on dolphin groups structure (Leatherwood and Platter footnote 10), with largest groups found offshore (Wells et al. 1980). However, criteria for defining "herds" or "subgroups" are rarely reported, and could influence differ-

ences in reported results. During our surveys we often encountered several herds within a few kilometers of each other, after not seeing dolphins for distances of 20 km or more. Although such assemblages may have been dispersed subgroups of a larger herd, they did not meet our arbitrary criteria for defining a "herd." Our spatial definition of herd may be unsatisfactory if bottlenose dolphins, like some other cetaceans, maintain acoustic contact over many kilometers (Payne and Webb 1971). Acoustic contact among free ranging groups of *T. truncatus*, however, has not been demonstrated, and we know of no more appropriate basis for defining herds from aerial sightings.

The proportion of dolphin calves noted during our surveys (5.3%) is low when compared with other reports. Leatherwood (1979) observed 8.1-10.1% calves during aerial surveys in eastern Florida in August, while Irvine et al. (footnote 8) reported a maximum of 11% from May to July during surface surveys near Sarasota, Fla. Shane and Schmidly (footnote 7) noted that calves constituted 7.6% of all dolphin sightings during surface surveys near Port Aransas, Tex., and Barham et al. (1980) sighted 9.3% calves from the air in the same area. Leatherwood[14] observed 7.7% calves in 1974 and 7.9% calves in 1975 near the mouth of the Mississippi River. Our calf counts may be lower because we only counted very small animals; calves may grow to 2 m long within the first year (Leatherwood footnote 14) and therefore large calves may not have been distinguished as such.

SUMMARY AND CONCLUSIONS

Most of the manatees (58.5%) were located in the Everglades National Park (Monroe County) and Ten Thousand Islands (Collier County) areas, and most (80.1%) were in brackish water. Because these areas are relatively undisturbed by human development, they have great value as locations to protect and study the endangered manatee.

Dolphins were well dispersed in the survey area. Fifty-one percent were sighted in the Gulf of Mexico, 49% were in brackish water, and none were located in freshwater.

Seasonal movement patterns and reproductive trends based on calf sightings of both dolphins and manatees are unclear. While the survey results are valuable as indicators of relative abundance, they are not useful to estimate total abundance because the percentage of animals not observed is unknown.

[14]Leatherwood, S. 1977. Some preliminary impressions on the numbers and social behavior of free swimming bottlenosed dolphin calves (*Tursiops truncatus*) in the northern Gulf of Mexico. *In* S. H. Ridgway and K. W. Benirshke (editors), Breeding dolphins: Present status, suggestions for the future, p. 143-167. National Technical Information Service PB 273 673.

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NOTES

EFFECT OF SEASON AND LOCATION ON THE RELATIONSHIP BETWEEN ZOOPLANKTON DISPLACEMENT VOLUME AND DRY WEIGHT IN THE NORTHWEST ATLANTIC[1]

Biomass or "standing stock" is a routinely measured index of abundance for studies of the interactions between trophic levels in the oceanic food web. Zooplankton biomass is usually reported as quantity of zooplankton per unit volume of water. Measures of quantity currently in use include displacement volume (Frolander 1957; Sutcliffe 1957; Yentsch and Hebard 1957; Tranter 1960; Ahlstrom and Thrailkill 1963), wet weight (Nakai and Honjo 1962), dry weight (Lovegrove 1966), and carbon (Curl 1962; Platt et al. 1969). These measures can be applied to a species at a specific developmental stage, to the entire population, or to all members of the community combined. Carbon and dry weight have been considered preferable because variability caused by interstitial and intracellular water is eliminated by either technique (Ahlstrom and Thrailkill 1963). They are not, however, practical measures in some investigations because specialized equipment is required and the techniques' destructive nature prevents further analysis of the sample. Measurement of displacement volume and wet weight are nondestructive, rapid, and use simple techniques which provide indexes of abundance, but do measure total matter, including water.

As an alternative, conversion factors or tables of "equivalents" have been used to transform displacement volume or wet weight into carbon or dry weight (Bsharah 1957; Menzel and Ryther 1961; Platt et al. 1969; Bé et al. 1971; Le Borgne 1975; Wiebe et al. 1975). However, plankton samples represent aggregations of organisms at a particular time and place which change according to season, geographical location, and local environmental conditions. For these reasons, and because many conversion factors were calculated with data produced by outdated techniques, the accuracy of interconversions between biomass measures has been questioned (Lovegrove 1966; Platt et al. 1969; Beers 1974). Recently, Wiebe et al. (1975) provided conversion factors based on data collected from different oceanic areas over several years in order to account for seasonal and geographical variation in samples.

This study explores whether a conversion equation based on data from numerous samples collected in contiguous areas during different seasons can account for sample variability and more accurately convert between biomass measures than equations derived from smaller and smaller subsets of data. Unlike previous studies, an intense sampling strategy provided the means to derive equations to convert between displacement volume and dry weight for samples from both broad and restricted geographic areas and for different seasons. Interconversion accuracy was verified with subsequent samples by comparing estimated values with field measurements. In addition, the relative variability and the values of both measures were compared in order to determine which index is more useful for these types of studies.

Materials and Methods

Plankton samples were collected by the National Marine Fisheries Service Northeast Fisheries Center in conjunction with the Marine Resources Monitoring Assessment and Prediction (MARMAP) program (Sherman 1980). Sampling was conducted six times a year in 1977 and 1978 off the northeast coast of the United States in three adjacent areas: Gulf of Maine (GOM), Georges Bank (GB), and Southern New England (SNE). Sampling locations are shown in Figures 1 and 2. Paired 61 cm diameter bongo samplers fitted with 0.505 mm and 0.333 mm mesh nets were towed obliquely through the water column at a speed of 1.5-2.0 kn. Maximum sampling depth was 200 m or 5 m from the bottom in shallower areas, and tow duration was 5-15 min. A flowmeter was strung inside the bongo frame to measure the volume of water filtered. Plankton samples from the 0.333 mm mesh nets were used in this analysis. Samples were preserved in 5% buffered Formalin[2] for at least 6 mo before anal-

[1]MARMAP Contribution MED/NEFC 81-8.

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

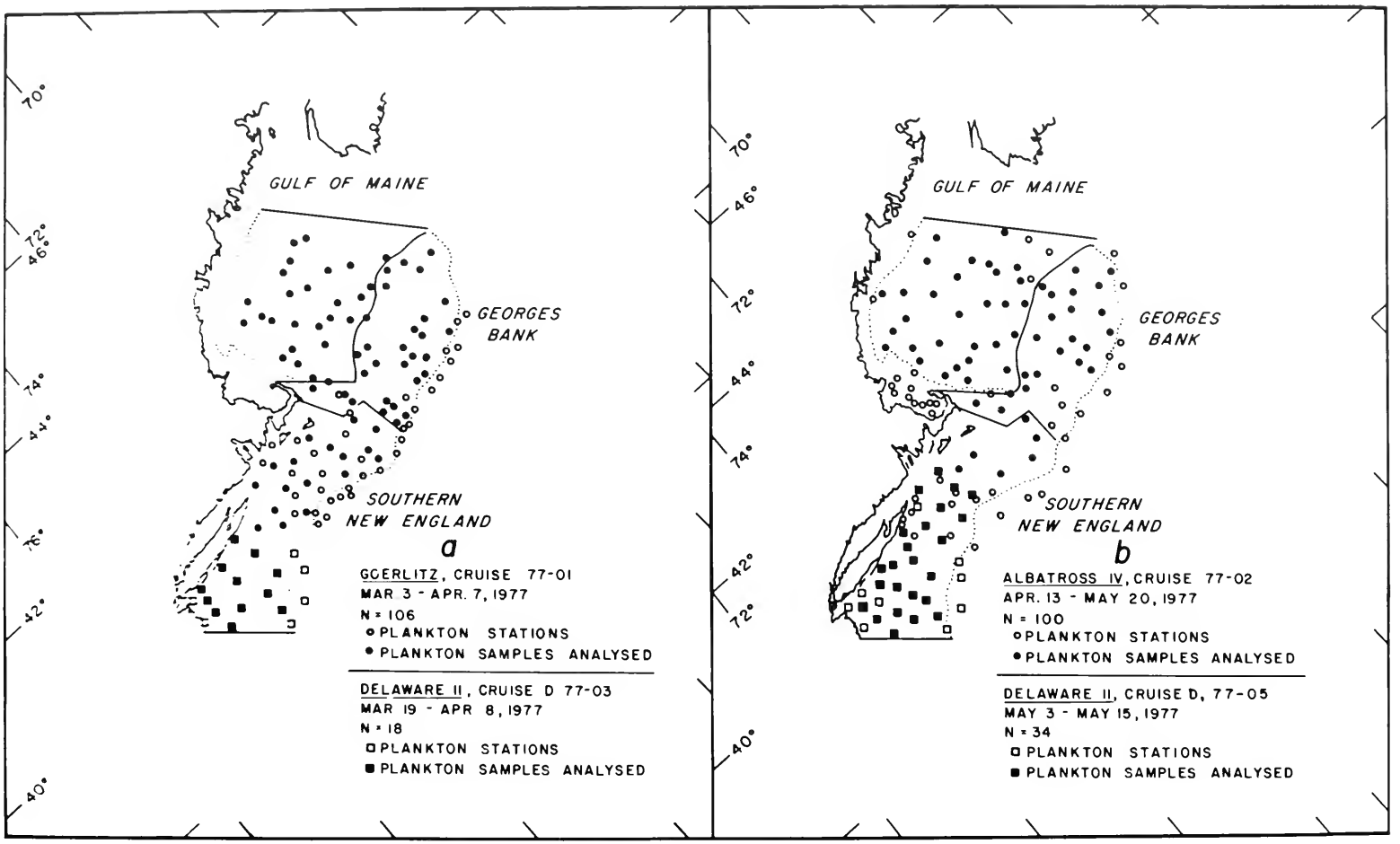

FIGURE 1.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1977.

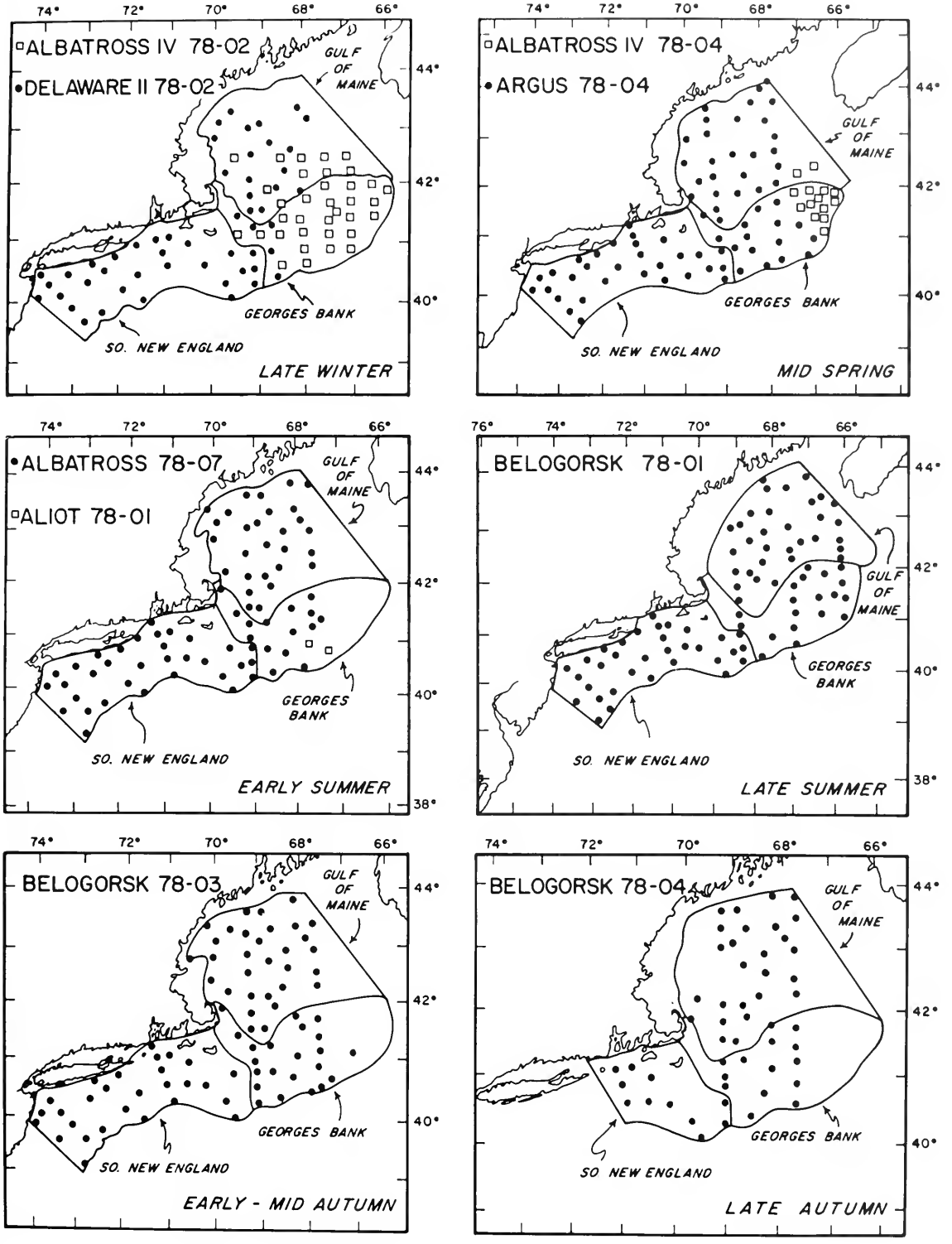

FIGURE 2.—Sampling locations and cruise numbers from the six seasonal MARMAP surveys for 1978.

ysis, sufficient time for the plankton to reach equilibrium volume and weight (Steedman 1976).

In the laboratory, displacement volumes were determined by using the technique outlined by Ahlstrom and Thrailkill (1963), with slight modifications. All organisms larger than 2.5 cm and nonplanktonic matter, i.e., small adult fishes, juvenile fishes, and seaweed, were removed prior to pouring the sample into a 1 l graduated cylinder, with 1 ml increments. After recording the volume, the sample was poured into a cone of 0.253 mm mesh suspended over a second graduated cylinder, and allowed to drain until the interval between drops was 15 s. The water volume was recorded. The difference between readings was recorded as the displacement volume. Dry weight was measured using the procedure outlined by Lovegrove (1966). Samples were dried at 60°C to a constant weight (2-5 d); a weight loss of 1 mg or less was considered constant. Samples were weighed to 0.01 mg on an analytical microbalance. Before analysis, all values were expressed as ml or gm/100 m^3 of water filtered and logarithmically transformed (base 10).

The geometric mean (GM) regression was used to express the relationship between displacement volume and dry weight because it is applicable to short series of measurements that have moderate or large variability, where the nature of error sources in the measurements is primarily natural, when compared with measurement error (Ricker 1973). The convention of using the GM regression for relating pairs of biomass measures was introduced by Wiebe et al. (1975), where a more detailed discussion of the theoretical and mathematical considerations of the GM regression as it applies to biomass measures is presented.

Using samples collected in 1977, conversion equations for displacement volume to dry weight were calculated using GM regressions for groups of measurements divided according to station and/or time of sampling as follows:

1) General: All measurements regardless of location or season (1).

2) Area: All measurements from a distinct oceanic region throughout the year (3).

3) Seasonal: Measurements within an area for a particular season (18).

Individual displacement volume readings from 1978 samples were converted to dry weight using each type of conversion equation. The predictive accuracy of the different equations was calculated by measuring the difference between the estimated and the directly measured dry weight, and expressing this difference as a percentage of the latter. The absolute values of the percent deviations for each conversion factor were then averaged for each group of seasonal and area-specific samples to determine which equation was most accurate. This method for evaluating different conversion factors was used instead of comparing differences between measured and estimated means because of the cancelling effect very high or low estimates would have on each other.

Results

A strong linear relationship exists between zooplankton displacement volume and dry weight (Table 1). Slopes of the GM regression lines were significantly different from zero ($P<0.001$), and correlation coefficients were high (0.885-0.977) for all lines within each class. The range of slope and elevation values for the 18 seasonal equations was significantly wide ($P<0.05$) to conclude that the different lines were not expressing the same biomass relationship. It was hypothesized that from among these regression lines there might exist discrete groups of significantly similar lines which could be combined to describe a fourth category of conversion equations. A Neuman-Keuls multiple range test (Zar 1974) pinpointed lines which differed significantly ($P<0.05$) in slope and/or elevation, but other lines could not be accurately assigned to distinct groups because of overlapping similarities. Increasing the amount of data might yield more acceptable conclusions, but it is more likely that these results reflect a gradient of changing trophic conditions which gradually alter the biomass relationship from season to season.

The seasonal class of conversion equations yielded significantly ($P<0.05$) more accurate estimates than either the general or areal equations. For the 18 groups of seasonal and areal samples collected in 1978, predicted dry weights on the average deviated 15.98% (range: 2.31-34.4%) from the actual values using the seasonal equations, as opposed to 29.27% (range: 12.62-66.34%) and 31.4% (range: 15.90-53.45%) for the areal and general equations, respectively. However, for certain seasons, the appropriate regression equation did not accurately convert dis-

TABLE 1.—Geometric mean regression equations calculated from 1977 displacement volume (DV) and dry weight (DW) measures for each area by season, each individual area, and for all values combined. Also included is the equation for phytoplankton-dominated stations.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
I Late winter-early spring	Log (DW) = −1.079 + 0.963 Log (DV)	27	0.951	0.00348
II Midspring	Log (DW) = −1.235 + 1.022 Log (DV)	30	0.900	0.00706
III Late spring	Log (DW) = −1.663 + 1.312 Log (DV)	30	0.956	0.00532
IV Midsummer	Log (DW) = −1.803 + 1.382 Log (DV)	34	0.890	0.0123
V Midautumn	Log (DW) = −1.190 + 0.976 Log (DV)	27	0.907	0.00672
VI Late autumn	Log (DW) = −1.245 + 1.006 Log (DV)	20	0.961	0.00476
All seasons	Log (DW) = −1.226 + 1.138 Log (DV)	168	0.943	0.000106
Georges Bank				
I Late winter-early spring	Log (DW) = −1.182 + 1.045 Log (DV)	28	0.885	0.00902
II Midspring	Log (DW) = −1.328 + 1.114 Log (DV)	23	0.929	0.00811
III Late spring	Log (DW) = −1.405 + 1.184 Log (DV)	27	0.930	0.00757
IV Midsummer	Log (DW) = −1.552 + 1.274 Log (DV)	21	0.898	0.0166
V Early autumn	Log (DW) = −1.622 + 1.296 Log (DV)	18	0.949	0.0104
VI Late autumn	Log (DW) = −1.210 + 1.091 Log (DV)	20	0.914	0.0111
All seasons	Log (DW) = −1.308 + 1.127 Log (DV)	137	0.954	0.000823
Gulf of Maine				
I Early spring	Log (DW) = −1.161 + 1.142 Log (DV)	13	0.960	0.00922
II Midspring	Log (DW) = −1.347 + 1.223 Log (DV)	21	0.954	0.00593
III Late spring	Log (DW) = −1.170 + 1.145 Log (DV)	27	0.947	0.00548
IV Midsummer	Log (DW) = −1.470 + 1.377 Log (DV)	28	0.966	0.00476
V Midautumn	Log (DW) = −1.201 + 1.242 Log (DV)	23	0.977	0.00339
VI Late autumn	Log (DW) = −1.747 + 1.514 Log (DV)	30	0.932	0.0108
All seasons	Log (DW) = −1.311 + 1.257 Log (DV)	142	0.963	0.00290
All areas				
Every season	Log (DW) = −1.383 + 1.207 Log (DV)	447	0.925	0.000484
Phytoplankton stations	Log (DW) = −1.481 + 1.016 Log (DV)	20	0.962	0.00910

placement volume to dry weight. It was found that a change in the biomass relationship occurred between years in the six seasons that predictive accuracy was lowest. This was determined by calculating regressions with 1978 data (Table 2) and comparing them with the corresponding 1977 seasonal equations. Year-to-year differences ($P<0.05$) in slope and/or elevation were evident for the following: GB early-mid-autumn, GB late autumn, GOM mid-late summer, GOM midautumn, SNE late winter, and SNE late spring-early summer. After perusal of sample contents, sampling dates, and sample species abundance, it was apparent that year-to-year changes in these factors were correlated with the 1977-78 differences in the regression equations mentioned above (Tables 3-5).

For those areas where no change in the relationship between displacement volume and dry weight occurred between years, data was com-

TABLE 2.—Geometric mean regression equations derived from 1978 displacement volume (DV) and dry weight (DW) values for each area by season and for samples with abundant siphonophore fragments.

Area/season	Regression equation	N	r	Variance of slope
Southern New England				
VII Late winter	Log (DW) = −0.795 + 0.725 Log (DV)	21	0.903	0.00810
VIII Midspring	Log (DW) = −1.287 + 1.088 Log (DV)	25	0.960	0.00620
IX Early summer	Log (DW) = −1.939 + 1.541 Log (DV)	30	0.969	0.00980
X Midsummer	Log (DW) = −1.802 + 1.388 Log (DV)	19	0.939	0.01900
XI Midautumn	Insufficient Data			
XII Late autumn	Log (DW) = −1.266 + 1.045 Log (DV)	10	0.927	0.0219
Georges Bank				
VII Late winter	Log (DW) = −1.229 + 1.095 Log (DV)	23	0.964	0.00941
VIII Midspring	Log (DW) = −1.515 + 1.238 Log (DV)	20	0.990	0.00260
IX Early summer	Log (DW) = −1.416 + 1.186 Log (DV)	16	0.900	0.0123
X Late summer	Log (DW) = −1.079 + 0.956 Log (DV)	18	0.881	0.0156
XI Midautumn	Log (DW) = −1.349 + 1.070 Log (DV)	20	0.945	0.00941
XII Late autumn	Log (DW) = −1.509 + 1.215 Log (DV)	14	0.950	0.0129
Gulf of Maine				
VII Late winter	Log (DW) = −1.158 + 1.148 Log (DV)	21	0.913	0.0219
VIII Midspring	Log (DW) = −1.137 + 1.085 Log (DV)	25	0.947	0.00865
IX Early summer	Log (DW) = −0.949 + 1.042 Log (DV)	27	0.927	0.00846
X Late summer	Log (DW) = −1.079 + 1.089 Log (DV)	22	0.949	0.00846
XI Midautumn	Log (DW) = −1.343 + 1.304 Log (DV)	24	0.957	0.0129
XII Late autumn	Log (DW) = −1.454 + 1.349 Log (DV)	20	0.875	0.0353
Siphonophore samples	Log (DW) = −0.975 + 0.773 Log (DV)	15	0.969	0.00397

TABLE 3.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Southern New England area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	N	r	Variance of slope
Late winter	Log (DW) = −0.795 + 0.725 Log (DV)	21	0.903	0.00810
Early spring	Log (DW) = −1.079 + 0.963 Log (DV)	27	0.951	0.00348
Midspring	Log (DW) = −1.103 + 0.929 Log (DV)	55	0.929	0.00348
Late spring	Log (DW) = −1.663 + 1.312 Log (DV)	30	0.956	0.00532
Early summer	Log (DW) = −1.939 + 1.541 Log (DV)	30	0.969	0.00980
Midsummer	Log (DW) = −1.795 + 1.379 Log (DV)	53	0.900	0.00757
Midautumn	Log (DW) = −1.190 + 0.976 Log (DV)	27	0.907	0.00672
Late autumn	Log (DW) = −1.251 + 1.109 Log (DV)	30	0.956	0.00360

B

Late winter		Early spring		Midspring		Late spring	
Copepoda	88.6	Copepoda	88.2	Copepoda	91.5	Copepoda	88.4
P. minutus	(87.8)	*P. minutus*	(75.1)	*C. finmarchicus*	(55.3)	*P. minutus*	(44.3)
C. finmarchicus	(6.2)	*C. finmarchicus*	(8.5)	*P. minutus*	(28.8)	*C. finmarchicus*	(37.2)
C. typicus	(3.0)	*T. longicornus*	(6.2)	*M. lucens*	(3.0)	*T. longicornus*	(11.7)
Chaetognatha	8.6	*C. typicus*	(5.4)	*A. longiremus*	(1.9)	*M. lucens*	(2.3)
		Cirripedia	9.6	*C. typicus*	(1.3)	Chaetognatha	6.3
				Chaetognatha	4.2	Cladocera	3.0
				Cladocera	1.4		

Early summer		Midsummer		Midautumn		Late autumn	
Copepoda	91.3	Copepoda	66.2	Copepoda	75.6	Copepoda	91.8
P. minutus	(33.9)	*C. typicus*	(59.8)	*C. typicus*	(70.1)	*C. typicus*	(60.6)
C. finmarchicus	(27.8)	*C. finmarchicus*	(19.8)	*A. clausi*	(5.1)	*P. parvus*	(15.3)
C. typicus	(19.0)	*P. minutus*	(5.2)	*A. tonsa*	(4.0)	*P. minutus*	(11.0)
T. longicornus	(11.6)	*M. lucens*	(3.1)	*P. minutus*	(3.4)	Chaetognatha	5.5
M. lucens	(1.2)	Cladocera	23.6	*P. parvus*	(3.2)		
Chaetognatha	7.8	Chaetognatha	4.5	*C. minor*	(2.2)		
		Thaliacea	1.7	Cladocera	21.3		
		Amphipoda	1.6	Chaetognatha	1.0		

TABLE 4.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Georges Bank area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	N	r	Variance of slope
Late winter-early spring	Log (DW) = −1.195 + 1.059 Log (DV)	39	0.908	0.00518
Midspring	Log (DW) = −1.324 + 1.119 Log (DV)	37	0.989	0.00372
Late spring-early summer	Log (DW) = −1.360 + 1.159 Log (DV)	40	0.954	0.00314
Midsummer-late summer	Log (DW) = −1.403 + 1.176 Log (DV)	36	0.891	0.00828
Early autumn	Log (DW) = −1.662 + 1.296 Log (DV)	18	0.949	0.0104
Midautumn	Log (DW) = −1.349 + 1.070 Log (DV)	20	0.945	0.00941
Late autumn (1977)	Log (DW) = −1.210 + 1.091 Log (DV)	20	0.914	0.0111
Late autumn (1978)	Log (DW) = −1.509 + 1.215 Log (DV)	14	0.950	0.0129

B

Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	80.7	Copepoda	89.7	Copepoda	76.6	Copepoda	89.3
P. minutus	(55.6)	*C. finmarchicus*	(79.8)	*C. finmarchicus*	(42.8)	*C. typicus*	(53.1)
C. finmarchicus	(37.1)	*P. minutus*	(16.9)	*P. minutus*	(36.1)	*C. hamatus*	(16.6)
C. typicus	(2.6)	*M. lucens*	(2.5)	*C. hamatus*	(11.7)	*C. finmarchicus*	(10.2)
M. lucens	(1.8)	Chaetognatha	2.3	*C. typicus*	(5.1)	*P. minutus*	(8.9)
Chaetognatha	6.9	Ostracoda	1.5	*M. lucens*	(1.5)	*P. parvus*	(5.6)
Cirripedia	4.9	Cirripedia	1.3	*T. longicornus*	(1.3)	*M. lucens*	(3.7)
Amphipoda	4.8	Amphipoda	1.1	Chaetognatha	6.7	Chaetognatha	4.9
Pelecypoda	1.7			Coelenterata	5.6	Cladocera	1.8
				Cladocera	4.1		
				Decapoda	3.1		

Early autumn		Midautumn		Late autumn (1977)		Late autumn (1978)	
Copepoda	95.1	Copepoda	94.5	Copepoda	86.6	Copepoda	89.8
C. typicus	(50.1)	*C. typicus*	(64.6)	*C. typicus*	(57.0)	*C. typicus*	(51.1)
P. minutus	(19.8)	*C. finmarchicus*	(10.2)	*P. minutus*	(28.0)	*P. parvus*	(19.9)
C. hamatus	(18.4)	*C. hamatus*	(8.7)	*C. finmarchicus*	(4.3)	*C. finmarchicus*	(11.0)
C. finmarchicus	(2.5)	*P. parvus*	(5.7)	*C. hamatus*	(3.8)	*P. minutus*	(7.9)
M. lucens	(2.0)	*P. minutus*	(5.6)	*P. parvus*	(2.2)	*C. hamatus*	(6.1)
P. parvus	(1.9)	*M. lucens*	(1.3)	*M. lucens*	(1.7)	Chaetognatha	8.7
Pelecypoda	1.7	Chaetognatha	2.3	Pelecypoda	6.9		
Chaetognatha	1.3	Amphipoda	1.4	Chaetognatha	5.5		

TABLE 5.—A) The recommended geometric mean regressions for interconversion between displacement volume (DV) and dry weight (DW) in the Gulf of Maine area; and B) the relative abundance of the major taxa (>1%) associated with the particular equation, expressed as percent of total numbers. Copepods are broken down into major species (>1%) with their abundance expressed as percent of total copepod numbers (in parentheses). Zooplankton data from Sherman et al. (1978, 1979).

A

Season	Regression equation	*N*	*r*	Variance of slope
Late winter-early spring	Log (DW) = −1.168 + 1.156 Log (DV)	25	0.956	0.00504
Midspring	Log (DW) = −1.169 + 1.106 Log (DV)	37	0.954	0.00314
Late spring-early summer	Log (DW) = −1.035 + 1.080 Log (DV)	47	0.949	0.00260
Midsummer	Log (DW) = −1.470 + 1.377 Log (DV)	28	0.966	0.00476
Late summer	Log (DW) = −1.079 + 1.089 Log (DV)	22	0.949	0.00846
Midautumn (1977)	Log (DW) = −1.201 + 1.242 Log (DV)	23	0.977	0.00339
Midautumn (1978)	Log (DW) = −1.343 + 1.304 Log (DV)	24	0.957	0.0129
Late autumn	Log (DW) = −1.576 + 1.419 Log (DV)	44	0.935	0.00608

B

Late winter-early spring		Midspring		Late spring-early summer		Midsummer	
Copepoda	96.3	Copepoda	93.5	Copepoda	94.0	Copepoda	97.5
C. finmarchicus	(63.7)	*C. finmarchicus*	(86.7)	*C. finmarchicus*	(83.5)	*C. finmarchicus*	(79.9)
M. lucens	(18.9)	*P. minutus*	(8.0)	*P. minutus*	(10.3)	*P. minutus*	(10.0)
P. minutus	(13.6)	*M. lucens*	(5.0)	*M. lucens*	(4.6)	*M. lucens*	(4.2)
Oithona sp.	(1.7)	Amphipoda	5.0	*A. longiremis*	(1.1)	*C. typicus*	(4.2)
Amphipoda	1.3			Cladocera	4.8	*A. longiremis*	(1.3)
						Cladocera	1.1

Late summer		Midautumn (1977)		Midautumn (1978)		Late autumn	
Copepoda	99.2	Copepoda	99.0	Copepoda	98.9	Copepoda	99.1
C. finmarchicus	(47.3)	*C. finmarchicus*	(51.3)	*C. typicus*	(39.1)	*C. typicus*	(37.0)
C. typicus	(42.0)	*C. typicus*	(29.3)	*C. finmarchicus*	(34.6)	*C. finmarchicus*	(28.3)
P. minutus	(7.7)	*P. minutus*	(11.4)	*P. minutus*	(17.9)	*P. minutus*	(21.4)
		M. lucens	(3.5)	*A. longiremis*	(1.5)	*P. parvus*	(4.7)
		P. parvus	(2.6)	*P. parvus*	(1.3)	*M. lucens*	(4.5)
						A. longiremis	(1.1)

bined and a new regression equation calculated. These equations, and the equations showing significant differences between years, are the recommended equations for conversion between the biomass measures (Tables 3-5). Choice of which regression to use should be based on area, season, and species composition. Confidence limits can be calculated for any predicted dry weight or displacement volume by using the method outlined by Ricker (1973) or Wiebe et al. (1975). A listing of values for predicting dry weights and displacement volumes within 95% confidence limits is given in Table 6.

The limitations of the method for the area under study are as follows. The presence in samples of organisms such as salps, jellyfish, and doliolids, which have a high displacement volume to dry weight ratio due to a greater retention of intracellular water, can significantly affect the accuracy of dry weight estimates (Wiebe et al. 1975). This was also observed in our data, but only on rare occasions were these organisms encountered. Chaetognaths were also mentioned by Wiebe et al. as organisms that could alter the biomass relationship. Since they are common, but not dominant, components of the plankton throughout the year in our sampling areas, the seasonal regressions account for their continuous presence and are therefore applicable to samples where they are present. This study revealed two additional situations in which sample composition caused a deviation in the biomass relationship. Twenty samples collected during late winter 1977 from the GOM and GB contained high concentrations of diatoms, primarily *Rhizosolenia* sp. and *Thalassiosira* sp., and microzooplankton not normally captured by 0.333 mm mesh nets. The samples resembled thick "pea soup" and many hours were required for draining in order to obtain a displacement volume reading. Since their dry weight to displacement volume ratios were very low compared with other samples collected during the same period, the samples were eliminated from the general analysis and a separate regression calculated ($r = 0.962$) for them (Table 1). The second situation was observed in autumn 1978 when the siphonophore population increased dramatically, especially off SNE and in the GOM. Since these delicate colonial aggregations are easily fragmented during collection, their abundance could not be measured quantitatively. For these samples, displacement volume to dry weight ratios were disproportionally high because of the intracellular water retained by their nectophores. The regression line calculated with data only from siphonophore-dominated samples was significantly different ($P<0.05$) in both

TABLE 6.—Values needed to calculate 95% confidence limits for predicted dry weights (DW) and displacement volumes (DV) from the equations in Tables 3-5. For an explanation of symbols and the methods used, one should consult Ricker (1973) or Wiebe et al. (1975).

Area/season	Prediction of DW				Prediction of DV		
	t_{95}	$\bar{X}'$	$\Sigma x'^2$	$Sy'x'^2$	$\bar{Y}'$	$\Sigma y'^2$	$Sx'y'^2$
Southern New England							
Late winter	2.05	1.329	4.384	0.0156	0.775	4.067	0.0168
Early spring	2.08	0.945	1.894	0.0154	−0.110	0.996	0.0292
Midspring	2.01	1.598	8.156	0.0281	0.478	9.250	0.0248
Late spring	2.04	1.915	2.025	0.0107	0.850	3.484	0.00622
Early summer	2.04	1.683	0.694	0.00671	0.655	1.651	0.00282
Midsummer	2.01	1.706	2.614	0.0205	0.577	4.973	0.0108
Midautumn	2.05	1.334	1.147	0.00780	0.117	1.092	0.0081
Late autumn	2.05	1.347	1.588	0.00568	0.121	1.648	0.00545
Georges Bank							
Late winter-early spring	2.02	0.962	3.363	0.0194	0.122	4.073	0.0173
Midspring	2.03	1.783	3.361	0.00309	0.671	4.918	0.00228
Late spring-early summer	2.02	1.892	5.938	0.0189	0.833	7.972	0.0141
Midsummer-late summer	2.03	1.615	1.730	0.0145	0.497	2.391	0.0105
Early autumn	2.10	1.471	0.652	0.00678	0.284	1.0952	0.00403
Midautumn	2.09	1.150	0.655	0.00615	0.256	0.748	0.00539
Late autumn (1977)	2.09	1.393	1.088	0.0119	0.310	1.2935	0.00997
Late autumn (1978)	2.15	1.492	0.767	0.00949	0.198	1.133	0.00676
Gulf of Maine							
Late winter-early spring	2.06	1.045	1.261	0.00630	0.041	1.685	0.00471
Midspring	2.03	1.571	2.037	0.00641	0.568	2.491	0.00524
Late spring-early summer	2.01	1.695	3.009	0.00772	0.796	3.508	0.00662
Midsummer	2.05	1.675	0.977	0.00470	0.836	1.851	0.00252
Late summer	2.12	1.396	1.738	0.00985	0.423	2.059	0.00832
Midautumn (1977)	2.07	1.708	1.446	0.0049	0.920	2.230	0.00317
Midautumn (1978)	2.16	1.501	0.232	0.00302	0.614	0.395	0.00177
Late autumn	2.01	1.592	2.552	0.0154	0.683	5.147	0.00766

slope and elevation from all other seasonal lines and had a high r value (Table 2). Since the occurrence of siphonophores in large numbers has been reported in our sampling areas (Sumner 1911; Rogers et al. 1978), this predictive equation should be useful for future occurrences of this phenomenon.

A coefficient of variation (cv) was calculated for each group of displacement volume and dry weight measures in order to compare the relative variability between the two indexes. As expected, both indexes were highly variable, with cv's averaging 54.3% (31.6-133.5%) and 65.4% (33.4-147.8%) for displacement volume and dry weight, respectively. Surprisingly, of the 36 data sets, 31 exhibited higher cv's for dry weight than for displacement volume. A two-tailed variance test was used to determine whether this difference was significant (Lewontin 1966) for the paired displacement volume-dry weight values. Only GOM late autumn (1977) displacement volumes had a significantly ($P<0.05$) lower cv than the corresponding dry weights. When all values were combined, however, and a single cv calculated for each index, displacement volumes were significantly ($P<0.05$) less variable. This was unexpected, because water retained interstitially and intracellularly should increase variability among displacement volumes. It appears, then, that displacement volume is a more consistent and more reliable measure of plankton standing stock than dry weight.

Zooplankton standing stock for 1977 and 1978 in each area is plotted in Figure 3A-C. The measures are juxtaposed in order to reveal whether any discrepancies exist between the two patterns. For SNE and GB the two indexes of abundance follow strikingly similar patterns. In the GOM, however, the dramatic midautumn increase in dry weight for 1977 is not equally reflected by the displacement volume curve. *Calanus finmarchicus* dominated these samples (Sherman et al. 1978) and further examination revealed that they were stage V copepodites, the condition in which they overwinter. Comita et al. (1966) showed that *C. finmarchicus* collected from the Bute Channel, England, reach their weight and caloric maxima in autumn and early winter, with stage V individuals having the highest values. The impact these overwintering preadults had on the dry weight measures was confirmed by plotting the seasonal mean dry weight-displacement volume ratios for all three areas (Fig. 4). GOM autumn ratios were highest for both years, 17.4% and 13.4%, respectively. Furthermore, samples dominated by *C. finmarchicus* had higher ratios than samples from shallower stations where the copepods *Pseudo-*

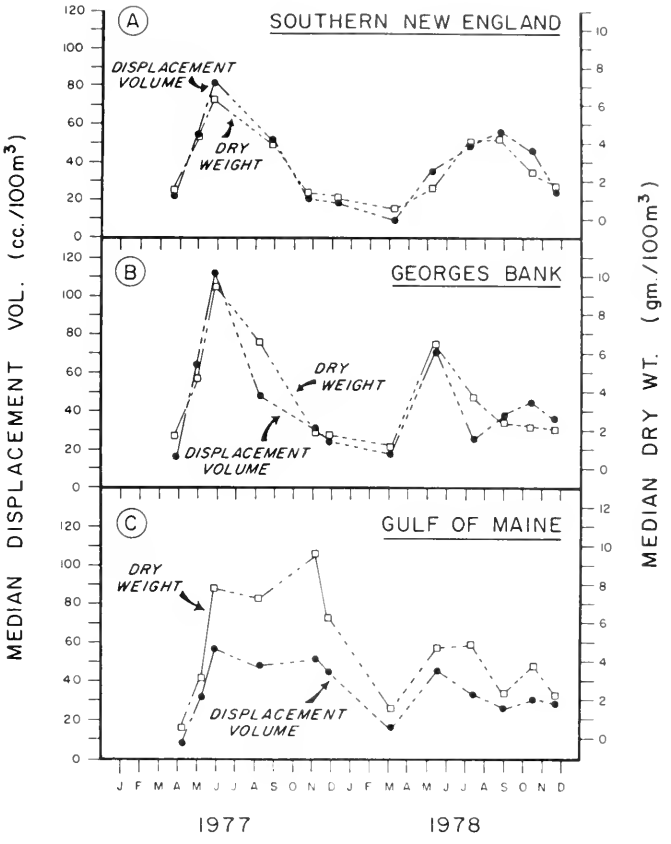

FIGURE 3.—Changes in median displacement volumes and dry weights for A) Southern New England, B) Georges Bank, and C) Gulf of Maine waters. Dashed lines represent intersurvey periods. Similar abundance trends are portrayed by both indexes, but discrepancies in magnitude between measures occur for Georges Bank summer samples and throughout the year in the Gulf of Maine. Displacement volumes are from Sherman et al. (1977, 1978).

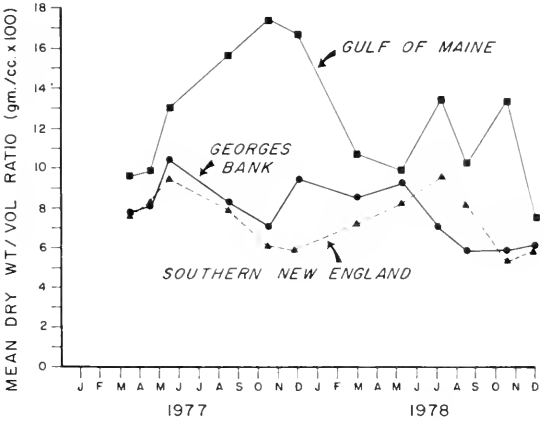

FIGURE 4.—Seasonal changes in dry weight/displacement volume ratios for the three sampling areas. Points are placed at the midpoints of the survey cruises. Gulf of Maine samples have higher values throughout the year.

calanus minutus or *Centropages typicus* were abundant. The preadult *Calanus* apparently store lipid reserves for survival through the winter and represent a substantial biomass underestimated by displacement volumes.

Autumn increases in dry weight were not observed for GB or SNE, though both areas support large populations of *Calanus* in the spring and summer. In general, overwintering *Calanus* remain in deep water and do not migrate vertically (Marshall and Orr 1955). The only concentrations of preadult *Calanus* found in these areas were at a few stations located near or below the 100 m contour line during late autumn. These samples had higher dry weight-displacement volume ratios than *Calanus* free stations. The GOM is able to support a large population of overwintering *Calanus* in deepwater basins.

Discussion

The linear relationship between displacement volume and dry weight is affected by the seasonal changes in species composition and age structure which occur throughout the year in zooplankton communities. Accurate interconversion between them is possible only with a ser-

ies of seasonal equations that are restricted to a specific area. A single general conversion equation derived from samples from a widespread area cannot provide estimates of abundance with sufficient accuracy to describe the variation in abundance and community composition necessary for detailed studies of trophic structure and community composition. The findings presented here are generally consistent with those of previous investigators (Lovegrove 1966; Platt et al. 1969; Beers 1974), with the exception of Wiebe et al. (1975). It should be recognized that the latter approach (Wiebe et al. 1975) has utility in comparing disparate data sets from different geographical areas and seasons. It is necessary to recognize the limitations of each approach and select according to the intended use of the data.

Previous reports have recommended dry weight determinations over displacement volumes because both interstitial and intracellular water is eliminated from the sample, removing bias caused by gelatinous organisms (Ahlstrom and Thrailkill 1963; Beers 1974). Further, since only organic and inorganic substances remain in the sample, dry weight should provide information regarding the potential food value of the plankton standing stock. However, the high correlation found between displacement volume and dry weight ($r = 0.925$, 442 df) implies that both measures provide equivalent assessments of standing stock and potential food value. In two of the three areas investigated, GB and SNE, both measures portray identical ascending and descending trends in biomass with maximal and minimal points closely correlated (Fig. 3). In addition, variability, though high for both techniques, is higher for dry weight.

Discrepancies between the two measures appear, however, when one examines GOM data. Standing stock is underestimated by displacement volume because samples there have high dry weight to displacement volume ratios (Fig. 4). As a consequence, when biomass is compared between the GOM and GB or SNE, each index gives a different interpretation of between-area differences (Fig. 5). For example, in autumn 1977, mean dry weight for the GOM was five times higher than for SNE, but mean displacement volume was only twice as high. This phenomenon is attributed to the life history of *C. finmarchicus* in the GOM. Dry weight values reported by other investigators from different areas are also more readily comparable than displacement volumes because Lovegrove's technique (1966) for measuring them has been widely accepted, while techniques for measuring displacement volumes vary, especially in the attempt to remove interstitial water (Wiebe et al. 1975). Thus, for studies comparing standing stock between different sea areas, and for other advantages previously mentioned, dry weight is the preferred measure.

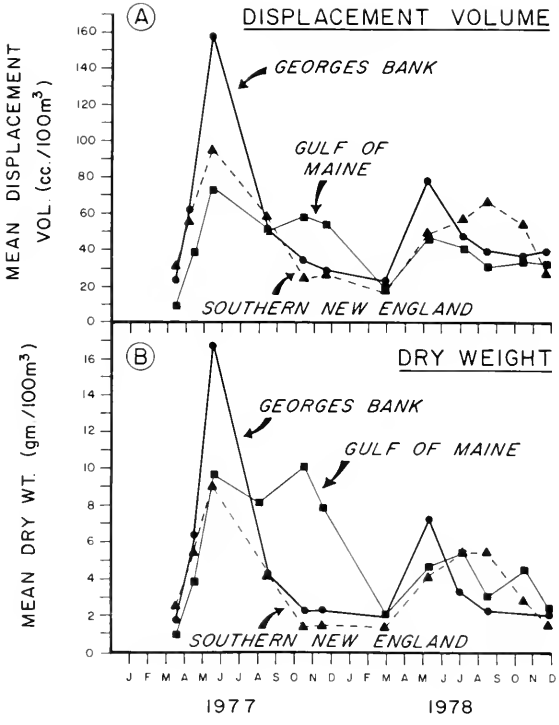

FIGURE 5.—Trends in plankton abundance for the three areas in 1977 and 1978 as measured by A) displacement volume, and B) dry weight. Each measure gives a different interpretation of between-area differences in biomass, especially in the Gulf of Maine.

Summary

This report has provided a series of season- and area-specific equations for the interconversion of zooplankton displacement volume and dry weight. In addition, interconversion equations for samples with large amounts of phytoplankton and siphonophore fragments have been calculated. However, dry weights should be measured directly on samples containing organisms with large amounts of intracellular water because they drastically affect the biomass rela-

tionship. It is our experience, however, that these organisms are abundant only on rare occasions in the MARMAP study area. The predictive equations should assist investigators assessing zooplankton standing stock on the continental shelf of the Northwest Atlantic.

General conversion factors at best yield only gross estimates, thus investigators should be aware of the limitations imposed by these values. A decision must be made by the investigator as to what level of accuracy is acceptable on the basis of what the data is to be used for. Further breakdown of the data into smaller subsets than area and season is possible, but the result would be an unwieldy number of equations sensitive to minute changes in trophic conditions. However, one can conclude from this study that effective displacement volume to dry weight conversion equations must to some extent take into account seasonal and areal variations in community composition. Given these considerations, the data presented here show no increase in variability inherent in displacement volume over dry weight biomass measures. Displacement volume provides a simple, easily routinized, rapid and nondestructive method of representing biomass, which is appropriate for processing the large numbers of samples typical of survey sampling programs.

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ESTIMATION OF EQUILIBRIUM SETTLEMENT RATES FOR BENTHIC MARINE INVERTEBRATES: ITS APPLICATION TO *MYA ARENARIA* (MOLLUSCA: PELECYPODA)

It is generally agreed that marine invertebrates possessing planktotrophic larval stages experience extremely high mortality during the early stages of their life history. In the settlement of benthic invertebrates, mortality occurs during three critical phases: 1) fertilization, 2) the free-swimming pelagic stage, and 3) the early postlarval attachment period. Since egg loss, larval recruitment, and early postlarval mortality may often be the limiting steps in the development and maintenance of marine benthic communities, it is of interest to ecologists to be able to make direct estimates of settlement rates in such populations.

It is often difficult, however, to obtain reasonable estimates of early life history stage mortality rates. The earliest attempt to determine such rates was made by Thorson (1966). Based on the standing crop of a population of *Venus* (= *Mercenaria*) *mercenaria*, he estimated that approximately 98.6% of the clams died during the postlarval period (stage 3) and that loss prior to this was probably much heavier. More recently, Muus (1973), in a study of 11 species of bivalves in the Oresund, Denmark, found postlarval mortality rates (stage 3) of 67-100% for all species; whereas Gledhill (1980) calculated larval mortality rates (stage 2) of 99.38% and 99.99% for two populations of *Mya arenaria* in Gloucester, Mass. None of these estimates, however, take into account the heavy mortality that occurs during stage 1, thereby overlooking the substantial loss occurring during the fertilization process itself.

In an attempt to overcome the difficulty in estimating early survival parameters empirically, Vaughan and Saila (1976) developed an indirect method using the Leslie matrix for determining mortality rates during the first year of life for the Atlantic bluefin tuna, *Thunnus thynnus*, assuming an equilibrium population. By expanding their treatment, as suggested by Van Winkle et al. (1978), it is possible to divide age class 1 into particular stages, thereby making the model appropriate for cases dealing with animals possessing more complex life cycles (i.e., those which include egg, larvae, postlarval juveniles, etc.). In the case of benthic invertebrates with free-swimming larval stages, this method can be used to calculate mortality rates during settlement for any species population for which demographic parameters are available. Such theoretical estimates are of special interest for two reasons. First, the equilibrium settlement rate (r_s) value can be compared with field-determined estimates; second, the value may be useful in the prediction of future age structures in natural populations.

This paper describes the indirect method for estimating the settlement rate based on age-specific fecundity and survivorship rates and discusses its application to a commercially important species of bivalve, *Mya arenaria*.

Results

Leslie Matrix

Matrix methods for analyzing age-structured populations were developed by Leslie (1945,

1948) and subsequently used in numerous studies of human and animal populations. In the present setting, the Leslie matrix takes the form:

$$L(r_s) = \begin{bmatrix} a_1 & a_2 & a_3 \ldots a_{n-1} & a_n \\ r_s b_1 & 0 & 0 \ldots 0 & 0 \\ 0 & b_2 & 0 \ldots 0 & 0 \\ . & . & . & . \\ . & . & . & . \\ . & . & . & . \\ 0 & 0 & b_{n-1} & 0. \end{bmatrix}$$

Here, a_i is the number of female eggs produced annually by a female *Mya arenaria* in class i (age $i-1$ to i), and b_i is the probability of a clam in class $i-1$ surviving to class i for $i \geqq 2$. The survivorship from age-class 1 to age-class 2 (P_0 in the notation of Vaughan and Saila (1976)) has been divided into two factors, r_s and b_1. The factor r_s is the settlement rate, or the probability that an egg will develop into a clam with a 2 mm shell length (0-2 mo of age); b_1 is the probability that a clam with a 2 mm shell length will survive the remainder of the year (about 10 mo).

The intrinsic growth rate is an increasing function of the settlement rate, r_s. Therefore, the equilibrium value, $r_{s_{eq}}$, $0 < r_{s_{eq}} < 1$, can be calculated for the population assuming steady state conditions. Since the values of a_i and b_i have been determined the *Mya arenaria* (Brousseau 1978a, b), $r_{s_{eq}}$ can be determined for this species. Similar calculations are described by Vaughan and Saila (1976) and Van Winkle et al. (1978).

Calculation of Equilibrium Settlement Rate and Stable Age Structure

Under conditions of the Perron-Frobenius Theorem, the population will reach an equilibrium state (starting with any initial reproducing population) if $\lambda = 1$ is the dominant eigenvalue of $L(r_s)$. Thus, $r_{s_{eq}}$ is the unique solution to the equation

$$|L(r_s) - \mathrm{I}| = 0.$$

By induction on the size of the matrix (n),

$$|L(r_s) - \mathrm{I}| = \pm (1 - a_1 - r_s b_1 a_2 - r_s b_1 b_2 a_3 - \ldots - r_s b_1 b_2 \ldots b_{n-1} a_n).$$

The required settlement rate is given by:

$$r_{s_{eq}} = \frac{1 - a_1}{b_1 a_2 + b_1 b_2 a_3 + \ldots + b_1 b_2 \ldots b_{n-1} a_n}.$$

Using the data in Table 1, the required settlement rate for *Mya arenaria* is $r_{s_{eq}} = 0.001462\%$ or 1 egg out of about 68,400 survive to 2 mm. Thus 1 egg out of 384,000 must survive the first year to maintain a steady population. Errors of up to 5% in the fecundity and survivorship values will yield equilibrium settlement rates of between 0.000983% (1 egg in 101,700 surviving to 2 mm size) and 0.00218% (1 egg in 45,800 surviving to 2 mm size). In addition, the eigenvector corresponding to the eigenvalue $\lambda = 1$ gives the stable age structure for the population. Postsettlement population structures were determined for only the $r_{s_{eq}}$ calculated above. The results are given in Table 2.

TABLE 1.—Life history statistics used in the derivation of the Leslie Matrix for *Mya arenaria*. (Data from Brousseau 1978b.)

Age (yr)	Age class	Shell length (mm)	Fecundity[1] (a_i)	Probability of survival (b_i)
0-1	1	2.0-29.9	0.0	0.177
1-2	2	30.0-44.9	3,744.0	0.912
2-3	3	45.0-59.9	17,170.0	0.904
3-4	4	60.0-64.9	31,159.0	0.952
4-5	5	65.0-69.9	39,957.0	0.949
5-6	6	70.0-74.9	50,341.0	0.969
6-7	7	75.0-79.9	62,460.0	0.984
7+	8+	80.0-84.9	76,465.0	0.911

[1]Fecundity = number of female eggs produced per individual, assuming a 1:1 sex ratio.

TABLE 2.—Calculated stable age structures for the population of *Mya arenaria*, based on the entire population and the adult population (≤30 mm) only.

Age class	Percent of entire population	Percent of adult population (≤30)
[1]1	42	
2	7	12
3	7	12
4	6	10
5	6	10
6	5	9
7	5	9
8	5	9
9	5	9
10	4	7
11	4	7
12	4	7

[1]This age class represents clams 2-29.9 mm in shell length.

Discussion

In his classic work on marine invertebrate communities, Thorson (1950) stated the definitive "number of eggs and larvae produced per pair of adult animals per lifetime to maintain the population is...one pair of larvae." More simply, to remain at equilibrium, a replacement rate of one must be maintained. For a population of *Mya*

arenaria possessing the life history statistics given above, 1 out of about 790,000 eggs produced during the lifetime of an individual must survive to ensure continuance of the population.

However, variable recruitment and high postlarval mortality tend to be the general rule among temperate and boreal marine invertebrates, especially the bivalves. At the Jones River in Gloucester, the tidal flat received a heavy set of young *Mya arenaria* in 1973 (Brousseau 1978a, b). Based on crude estimates of stock density, age-specific fecundity, and the density of the resultant spatfall, the settlement rate was 0.0498%, or about 34 times larger than the calculated $r_{s_{eq}}$. During the two subsequent years, on the other hand, this site received only a limited spatfall, which, coupled with high postlarval mortality, resulted in settlement rates of 0.0%. Under such fluctuating conditions, therefore, the settlement history of a population takes on added significance.

In addition to being of theoretical interest, determination of the equilibrium settlement rate for a commercially important species may be of value in its harvesting management as well. Although the impact of repeated exploitation is difficult to assess given the uncertainties of environmental conditions, continued harvesting on tidal flats receiving annual settlement rates below equilibrium may prove to be extremely harmful to the resident population.

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GROWTH OF JUVENILE RED SNAPPER *LUTJANUS CAMPECHANUS*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The red snapper, *Lutjanus campechanus*, has received considerable attention in the past due to its importance as a commercial and sport fish in the Gulf of Mexico. Most published material deals with the fishery and is summarized in Carpenter (1965). Few major papers have dealt with the natural history of red snapper.

Moseley (1965) reported on growth, reproduction, and food habits of red snapper taken by trawl and handline off the Texas coast. He determined age and growth rate from scales by assuming that growth checks were produced during the spawning season. Bradley and Bryan (1975) also sampled red snapper along the middle Texas coast with trawl and hook and line. They were unable to distinguish age classes by length frequencies and attributed that to an extended spawning season. Futch and Bruger (1976) used otolith readings to determine age and growth of red snapper off the coast of Florida.

This paper presents new information on growth of young snapper and relates that information to their occurrence on an artificial reef.

[1]University of Texas Marine Science Contribution No. 519.

Study Area and Methods

The artificial reef, composed of three sunken World War II liberty ships, is located approximately 29 km offshore (lat. 27°35'N, long. 96°54'W) from Port Aransas, Tex., in 33 m of water. Red snapper were collected from the reef with fish traps in March, May, July, September, November, and December 1979. The rectangular traps (1.8m × 1.2m × 0.6m) were made of 1.25 cm reinforcing bar covered with 3.4 cm mesh plastic coated wire. The entrance cone had an initial opening of 60.9 × 45.7 cm terminating in a 90° downturn with a 25.4 cm diameter entrance port. During each sampling period, five traps were baited with fish scraps and set on the bottom around the reef for 24 h. All red snapper captured in traps were measured in standard and total lengths and placed in a flowing seawater live box onboard ship. Snapper which were in good condition after 1 h on board ship were tagged with numbered internal-anchor tags and released over the artificial reef.

Small red snappers (<160 mm) were collected from the south Texas outer continental shelf during 1975 through 1977 with a 10.7 m "flat trawl" with 4.45 cm stretch mesh in the body and 2.5 cm stretch mesh in the bag. From 1975 to June 1976 a 9.5 mm stretch mesh liner was used inside the bag. Trawl sampling depths ranged from 10 m to 132 m. Seventy-two trawl samples were taken in 1975, 222 in 1976, and 294 in 1977. All trawls were made at a speed of about 2 kn for 15 min. (For details of sampling sites and procedures see Flint 1981.)

Results

Growth

The smallest fish taken in the trawl samples were generally 20-29 mm (Table 1). Juveniles <40 mm were caught in August, September, and October, and eight individuals of this size were taken in June 1976. Two year classes can be identified in the length-frequency table (Table 1) and followed for 12-18 mo. The smallest fish taken in traps at the ship reef were 100-110 mm. Snapper <100 mm could escape through the mesh.

Length-frequency histograms for combined trawl and trap data are shown for each month (Fig. 1). Two cohorts, age group 0 and age group I, are apparent in the data and a third cohort, age group II, may be present in the March and July data.

Recruitment of small snapper (<40 mm) into the population occurred primarily in June and July as evidenced by the modal size of the age 0 year class in August, September, and October. Limited recruitment of small fish continued into October. Length-frequencies of snappers captured in June through December were distinctly bimodal. Modal size classes for age I fish were 110 mm in June and 130 mm in July. Modal size classes for age I+ fish were 150 mm in December

TABLE 1.—Length-frequency distribution of red snapper caught in trawl samples. The number of individuals of each size class in each month is shown. No samples were taken in months with an asterisk (*).

	1974	1975												1976											1977									
Length	D	J	F*	M*	A	M	J*	J*	A	S	O*	N*	D*	J*	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D
10-19																			1																		
20-29									2	12									6																		
30-39									1	4									1			1	5														
40-49	1								7						1							3	12	6	1									2	3		
50-59	2								8	1						1						11	1	7	1	1								11	10		
60-69	5				1				3	1					11							1	3	3			1		1					24	11	1	
70-79	4				4				4	4					6							4	7						8					26	20	1	1
80-89	1	1			1	1			1	3					3				1			13	3	3				1	5					27	16	2	
90-99	2					2									6	2	2		2			9	4		1				2	4				5	2		
100-109	1															2			2			1					1			4				2	2	1	
110-119						1									2				2											5	2					1	1
120-129	1														1				1											3							
130-139	1														3				1																		
140-149																					1	2													1		
150-159																1						1												1			
160-169																				1	1						1										
170-179																				3		1					2	1							2		
180-189																												3									
190-199																						1						5									
200-209																					1							3									
210-219																												1									
220-229																												2									
230-239																												1									

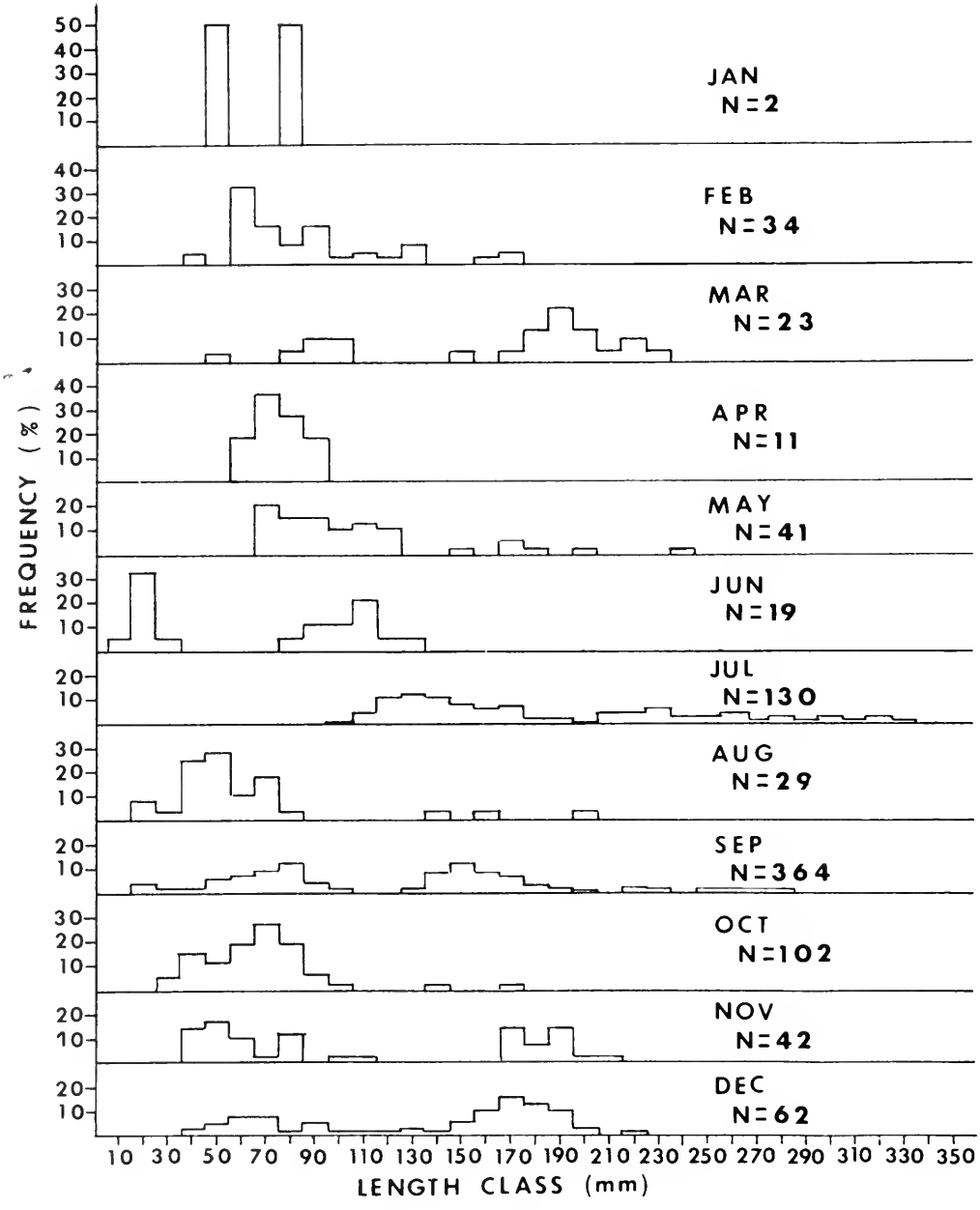

FIGURE 1.—Size distribution of young red snapper from pooled trawl and fish trap collections.

and 190 mm in March. It appears that age II snapper were 210-230 mm in July although few fish of that age class were caught.

Tagging

Numbered, internal-anchor tags were placed in 267 red snapper between 117 and 350 mm (mean = 192 mm) on the ship reef in July, September, and November 1979. Sportfishermen returned 28 tags and our fish trap sampling produced seven additional returns (13% total return rate). All fish were recaptured from the ship reef. The longest "free time" for any fish in our study was 92 d except for one fish which was tagged and recaptured twice over a 112-d period.

Sixty-three percent of the recaptures were within 30 d of release. No fish were recaptured after 11 December 1979 despite continued fishing effort on the ship reef during the winter and spring of 1980.

Measurements from the seven fish recaptured by our own sampling yielded growth rates of 0.12-0.55 mm/d (mean = 0.29 mm/d). Based on age determination from our length-frequency plots, these represent growth rates of age I+ snapper. Lengths of recaptured red snapper reported by sportfishermen were not considered accurate enough to use for growth determinations.

Discussion

Bimodal size distributions of red snapper caught in trawls and traps indicate that juvenile red snapper grow more slowly than previously thought. Moseley (1966) presented the first detailed account of growth rates for snapper using scale annuli for age determination. He assumed that growth checks were produced during the spawning period rather than during a midwinter slow growth period, an assumption confirmed by later workers (Futch and Bruger 1976). Moseley (1966) found that fish with one spawning check averaged 250 mm and determined a growth rate of about 90 mm between spawnings (about 0.25 mm/d). He proposed that red snapper grow 200-230 mm during their first year. Bradley and Bryan (1975) cited other unpublished data from Texas which indicated an initial growth check on scales at about 200 mm fork length and a mean growth rate of 60 mm/yr between formation of the first and the fifth rings. Futch and Bruger (1976) determined that maturity is probably reached after the second year (age II+) in Florida. Their data also indicated that the first growth check (on otoliths) generally occurred on snapper of about 200 mm.

A slower growth rate could be inferred from otolith, scale, and vertebrae aging by Bortone and Hollingsworth (1980) who found that snapper with one growth check averaged 163 mm and snapper with two growth checks averaged 197 mm. Small sample size (46) and one sampling date (17 October) may have influenced their results. That snapper mature at age II+ (Futch and Bruger 1976) and produce growth checks as a result of spawning activity suggest that fish with a single annulus are not age I+ as Moseley (1966) suggested but are age II+. Our data are consistent with this hypothesis. The distinct bimodality in length frequencies of snapper <220 mm during June through December (Fig. 1) indicates the presence of two year classes within this size range. We propose that red snapper grow to 110-130 mm during the first year and attain a size of 220-230 mm the second year. It is at this size (age II) that they apparently reach sexual maturity (Camber 1955; Futch and Bruger 1976). This growth rate is consistent with established postspawning growth rates of 60 (Bradley and Bryan 1975) to 90 mm/yr (Moseley 1966) between the first and fourth or fifth spawnings.

Red snapper >160 mm were uncommon in our trawl samples. Bradley and Bryan (1975) also collected few snapper between 150 mm and 220 mm in trawl or hook and line catches. Numerous fish of this size were trapped at the ship reef in July and September. Tagging data indicated that 130-250 mm (age I and early age II) snapper were abundant on the ship reef from July through September and some remained there through November or December. The absence of tag returns after December indicates that the fish present there all summer and fall either moved away, presumably to deeper water (Moseley 1966; Bradley and Bryan 1976) or had suffered substantial mortality. Fable (1980) found essentially no movement in 17 returns from 299 tagged red snapper in 60 m of water off the Texas coast.

Conclusions

1. We suggest that growth rates of juvenile red snapper during the first 2 yr are slower than previously reported. Our data indicate snapper attain a length of 110-130 mm the first year and 200-230 mm the second year.
2. Juvenile snapper <150 mm were common in trawl samples throughout most of the year.
3. Snapper 130-250 mm were common on the artificial reef from July through December. Tagging studies indicated the snapper remain around the artificial reef during the summer and fall but none were captured there or elsewhere after December.

Acknowledgments

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AN ASSOCIATION BETWEEN A PELAGIC OCTOPOD, *ARGONAUTA* SP. LINNAEUS 1758, AND AGGREGATE SALPS

Biologists working in the epipelagic zone of the ocean have reported that representatives of numerous planktonic taxa seem to be closely associated with gelatinous zooplankton, including hyperiid amphipods (Madin and Harbison 1977; Harbison et al. 1977; Laval 1980), gammarid amphipods (Vader 1972), isopods (Barham and Pickwell 1969), decapods (Shojima 1963; Thomas 1963; Trott 1972; Bruce 1972; Herrnkind et al. 1976), cyclopoid copepods (Heron 1973), mysids (Băcescu 1973), cirripedes (Fernando and Ramamoorthi 1974), and fish (Mansueti 1963; Janssen and Harbison in press).

Some symbionts in these groups are morphologically adapted to feed principally on the host and/or on the food material which the host collects, while others seem to associate more intermittently with gelatinous zooplankton, dependent on their nutritional state and that of the gelatinous hosts. Accordingly, symbioses may range from specific, structural associations to temporary or casual associations.

In this note we report a previously undescribed association between a cephalopod and a planktonic gelatinous herbivore. While conducting research scuba studies of gelatinous zooplankton in the western Gulf of Mexico, we collected juvenile pelagic octopods of the genus *Argonauta* sp. Linnaeus 1758, in association with aggregate generation salps (*Pegea socia* (Bosc 1802)).

The salp chains were composed of 40-60 individuals, each approximately 10 cm in apical/basal length. Individuals within the aggregate generation of *Pegea socia* (Bosc 1802) are uniformly covered with fine reticulated gold pigmentation and contain orange nucleii. The individuals each have four noticeable body muscles forming two x-shaped groups. Within each group, the pair of muscles are not fused dorsally. Endostyle bands of each individual are slightly arched.

Two juvenile octopods, a male and female with mantle lengths 8.4 mm and 6.7 mm, respectively, were collected from separate chains at a depth of 5-10 m at lat. 26°21′N, long. 95°45′W, on 26 February 1981. The males and females of *Argonauta* sp. have eight circumoral appendages, none of which are filiform. The body is not flattened, has no fins and no aquiferous pores on the head. The dorsal arms of the female are not

connected by a deep web and have broad terminal expansions modified for secretion of an external shell of egg case when mature. The left third arm of the male is hectocotylized, autonomous, and coiled up in a sac beneath the left eye.

The octopods were first noted inside the branchial cavity of one of the aggregate salps, attached by their tentacles to that individual's pharynx wall; however, they both left their hosts during our capture of the salps in quart jars. We found only one octopod per salp chain, though the salps had many hyperiid amphipods (*Vibilia armata* Bovallius 1887), cyclopoid copepods (*Sappharina angusta* Dana 1852), and fish in association. We found no morphological damage to the individual aggregate salps which had hosted the octopods.

The association of juvenile octopods with salp aggregates may afford a source of food (commensal amphipods), flotation, transportation, and/or camouflage to the octopods. Examination of Formalin[1]-preserved gut contents from these octopods was inconclusive, however, since neither octopod had fed recently and only unidentifiable, residual solids remained in the gut. It is improbable that the octopod was seeking protection by attaching to the salp chain, since moving out from the host was an immediate reaction to in situ visual stimuli and/or local perturbations.

We thank C. E. Lea and G. J. Denoux for their identification of the octopods and copepods, respectively. Identification of the octopods was based on generic characteristics described by Voss (1956). Salps were classified as *Pegea socia* (Bosc 1802) as described by Madin and Harbison (1978). Amphipod identification was based on body shape, eye structure, and character of pereiopods as described by Bowman and Gruner (1973) for genus and Dick (1970) for species. Copepods were identified by body shape, segmentation, and appendage characteristics as described by Owre and Foyo (1967). Research scuba operations were supported by the National Science Foundation, grant OCE78-22481.

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MIGRATION OF A JUVENILE WOLF EEL, *ANARRHICHTHYS OCELLATUS*, FROM PORT HARDY, BRITISH COLUMBIA, TO WILLAPA BAY, WASHINGTON

Juvenile wolf eels, *Anarrhichthys ocellatus*, were rarely reported off the Washington-Oregon coast prior to 1979. One 87 mm juvenile was collected by midwater trawl in 1962, 80 km off Newport, Oreg. (Wakefield 1980[1]). Another juvenile of 468 mm standard length (SL) was caught in 1969 (51 sets) by personnel of the Northwest and Alaska Fisheries Center, National Marine Fisheries Service (NMFS), while purse seining for juvenile salmonids in shallow marine waters (<30 m in depth) adjacent to the mouth of the Columbia River.

While purse seining for juvenile salmonids in these same waters, no wolf eels were caught in either 1978 (49 sets) or 1980 (67 sets) by NMFS, but in 1979 (109 sets), 19 specimens between 467 and 531 mm SL were collected. Oregon State University (OSU) personnel caught 113 juveniles during a 10-d purse seine cruise for juvenile salmonids in 1979 (56 sets) between the Columbia River and Coos Bay, Oreg., in waters >30 m. These fish ranged in size from 281 to 610 mm SL (Wakefield 1980). The purse seine used in waters <30 m deep fished to a depth of about 6 m (verified by the author using scuba). Based on its construction, the purse seine used in waters >30 m by both NMFS and OSU was assumed to fish to about 24 m deep.[2]

Personnel of NMFS, fishing in waters >30 m, collected seven juvenile wolf eels in 1980 (232 sets) between Copalis Head, Wash., and Tillamook Bay, Oreg. These fish ranged in length from 430 to 506 mm SL.

One of these juvenile wolf eels had been tagged on 24 October 1978 off Doyle Island near Port Hardy, British Columbia (Fig. 1), by personnel of the Canadian Department of Fisheries and Oceans (Bailey[3]). The tag was applied incidentally to a purse seine tagging operation for chum

[1]Wakefield, W. W. 1980. Occurrence and food habits of pelagic *Anarrhichthys ocellatus* juveniles collected off the Oregon coast during June, 1979. Paper presented at Sixtieth Annual Meeting of the American Society of Ichthyologists and Herpetologists at Texas Christian University, Fort Worth, Texas, June 15-20, 1980.

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[3]D. D. Bailey, Chief, Salmon Services, Department of Fisheries and Oceans-Pacific Region, 1090 West Pender St., Vancouver, British Columbia V6E 2P1, pers. commun. August 1980.

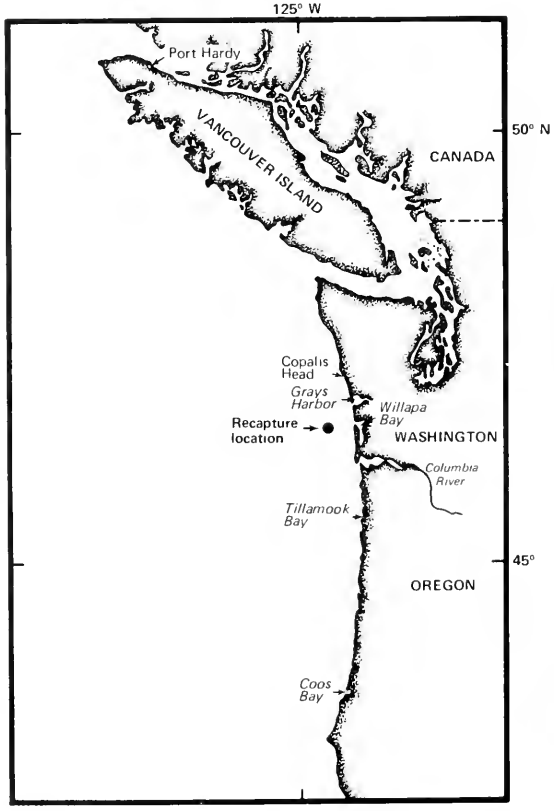

FIGURE 1.—Location of tagging (Port Hardy, B.C.) and recapture (Willapa Bay, Wash.) sites of a juvenile wolf eel.

salmon, *Oncorhynchus keta*. Only one wolf eel was tagged and its length was not recorded (Gould[4]). The juvenile was recaptured on 12 July 1980, 23 km off Willapa Bay, Wash., and was 502 mm long (Fig. 1). Distance traveled from tagging location to recapture site was about 593 km in 628 d. Approximate average movement was 0.94 km/d.

Information about the early life history of wolf eels has been sparse. Kanazawa (1952) and Marliave (1978) both observed a change to adult characteristics of pigmentation and dentition at lengths between 500 and 600 mm SL. Marliave, who has reared wolf eels at the Vancouver Public Aquarium in British Columbia, placed the juvenile-adult changeover at the end of the first year of life. He also noted that the fish, by the age of 3 mo, had begun to prefer the bottom except when feeding. Shelter seeking and territoriality became evident between 4 and 5 mo of age and about 200-400 mm long. At the end of 15 mo the fish ranged from 600 to 950 mm in length with a mean of just under 700 mm.

The tagged juvenile specimen has provided the first evidence of a difference in early life history of wild wolf eels compared with aquarium-reared fish with regard to juvenile behavior, growth rate, and length of time in the juvenile phase. This wolf eel possessed juvenile characteristics of coloration and dentition and was a minimum of 2+ yr in age. It was pelagic and below the lower end of the growth range attained by aquarium fish in 15 mo.

There have been no reports in the literature documenting migratory behavior of this species. Adult wolf eels are known to exhibit strong territoriality and attraction to some type of structure as shelter. Also a strong homing instinct exists even though a considerable amount of territory is covered while feeding away from shelter (Hulberg and Graber 1980).

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Fishery Bulletin

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

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IN MEMORIAM

Thomas A. Manar

1912-1982

Thomas Alonzo (Lon) Manar, former Chief of the Scientific Publications Staff (now the Scientific Publications Office), died at his home in Encinitas, Calif., on 26 August 1982 after a heart seizure. Lon Manar was a journalist, newspaperman, science writer, and editor in the best traditions of his craft. As the Chief of the Scientific Publications Staff in Seattle, Wash., from 1970 to 1974, he set the style and format for a revamped U.S. Fishery Bulletin. The early years of the Marine Fisheries Review also reflected his flair for innovative and creative journalism. In 1974 his superior service and unique talents were recognized with the award of a Bronze Medal by the U.S. Department of Commerce.

A graduate in journalism from the University of Oklahoma, Mr. Manar joined the Scripps Institution of Oceanography as scientific editor in 1951 after a stint as a meteorologist in the U.S. Army during World War II and as a newspaperman in Oklahoma. In the early 1960's he set up the public information office at the University of California, San Diego when the campus was developing.

In 1965, following the death of his wife, Ruth, Mr. Manar left the University for a position with the Federal Government as Chief of Publication Services for the Bureau of Commercial Fisheries Biological Laboratory in Honolulu, Hawaii; until 1970 he lived and worked in Honolulu. His last position before retirement was as an editor and consultant with the Southwest Fisheries Center of the National Marine Fisheries Service, NOAA, in La Jolla, Calif.

Mr. Manar was a man of wide interests and enthusiasm—art, music, reading, nature photography. After his retirement he traveled extensively in this country and abroad. He is survived by a sister, Maurine Manar of Encinitas.

While Mr. Manar was not a fishery biologist, he understood scientists and their needs. Many manuscripts arrived on his desk in shambles and emerged as examples of good scientific writing. Those of us who benefited from his talents are grateful; the Fishery Bulletin has benefited the most.

QUALITATIVE AND QUANTITATIVE NUTRIENT REQUIREMENTS OF FISHES: A REVIEW[1]

MARK R. MILLIKIN[2]

ABSTRACT

Qualitative and quantitative protein, amino acid, lipid, fatty acid, carbohydrate, vitamin, and mineral requirements are summarized for salmonids and warmwater fish species. Special emphasis is placed upon amino acid, vitamin, and mineral requirements of fishes, since recent research with these nutrients has contributed to a better understanding of fish physiology and nutritional requirements. Protein requirements of fishes briefly stated are as follows: 30 to 55% dietary protein dependent upon age and feeding habit and dietary essential amino acids which include arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine. Dietary lipid concentrations as high as 12 to 24% have demonstrated sparing action of protein for growth rather than energy utilization in fishes. Essential fatty acids for fishes usually include linolenic acid or an elongated form in the $\omega 3$ fatty acid family, while some fish species appear to derive nutritional benefit from linoleic acid. Vitamins required by fishes in the diet include thiamine, riboflavin, pyridoxine, niacin, pantothenic acid, ascorbic acid, choline, folic acid, cyanocobalamin, biotin, inositol, vitamin A, cholecalciferol, vitamin E, and vitamin K. Minerals required in the diet of fishes include phosphorus, magnesium, and trace amounts of manganese, zinc, iron, copper, selenium, and iodine. Carbohydrate is an important dietary energy source for herbivorous and omnivorous species and can be incorporated into diets of carnivorous species for protein sparing action at slightly higher concentrations than those occurring in their natural diets.

A paucity of information exists concerning qualitative and quantitative nutrient requirements of various life stages of several species currently reared in large quantities in fish hatcheries. Interactions of various macronutrients and micronutrients as related to artificial diet formulation for fish culture are also discussed. Additionally, recommendations for future research are outlined.

Determination of nutrient requirements for fishes fed formulated diets has contributed to healthier, more rapidly growing fishes cultured in hatcheries and commercial facilities. For instance, formulated diets designed specifically for several salmonid species and channel catfish, *Ictalurus punctatus*, have been instrumental in the recent growth of salmon, trout, and catfish commercial culture. Recent production values of catfish, trout, and salmon by aquaculture in the United States are listed in Table 1. Information has also been gained on many physiological similarities and differences between fishes and other aquatic and terrestrial species.

Reviews dealing with nutrient requirements of fishes include those by Halver (1972a) and the National Research Council (1973, 1977, 1981). Halver (1972a) dealt with macro- and micronutrient requirements of fishes, known and proposed biochemical pathways in fishes, feed formulation strategy, fish cultural practices, and feeding aspects of fish culture. However, since this thorough description of nutrient requirements of fishes, much additional information has been gained on fish nutrition. Synopses have been compiled of chemical composition of feed ingredients commonly used in formulated fish feeds, recommended test diet ingredient composition for determination of nutrient requirements of fishes, and feed formulation strategies on use of various combinations of protein or lipid sources (National Research Council 1973, 1977, 1981). Brief reviews of qualitative and quantita-

TABLE 1.—United States aquaculture production of catfish, trout, and salmon, 1979 and 1980.[1]

Species	1979		1980	
	Metric tons	Thousands dollars	Metric tons	Thousands dollars
Catfish	18,415.9	28,800	34,790.6	53,600
Salmon	1,088.6	900	3,447.3	3,400
Trout	11,339.8	21,000	21,772.5	37,500

[1]Adapted from Thompson (1981). Data represent live weight harvest for consumption. Excluded are eggs, fingerlings, and other intermediate products.

[1]Contribution No. 82-13C, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Charleston, S.C.

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tive nutrient requirements for specific groups of fishes are available. Included are those for trout, salmon, and catfish (National Research Council 1973), warmwater fishes such as common carp, *Cyprinus carpio*, channel catfish (National Research Council 1977), and salmonids (National Research Council 1981). Cowey and Sargent (1979) reviewed recent advances in protein, lipid, amino acid, fatty acid, vitamin, and mineral requirements of fishes, since their earlier work (Cowey and Sargent 1972). Special emphasis was placed on biochemical pathways in fish. However, only selected vitamin and mineral nutrient requirements of fishes were discussed, and no attempt was made to summarize, in total, the nutrient requirements of fishes. Also, a brief review of qualitative amino acid, fatty acid, vitamin, and mineral requirements of fishes is available in tabular form (Ketola 1977).

Currently, there is a paucity of information on nutrient requirements of fry and fingerling stages of coolwater fishes having commercial or recreational value (Ketola 1978; Orme 1978). Such species include the largemouth bass, *Micropterus salmoides*; smallmouth bass, *M. dolomieui*; yellow perch, *Perca flavescens*; northern pike, *Esox lucius*; muskellunge, *E. masquinongy*; tiger muskie hybrid (male northern pike × female muskellunge); and walleye, *Stizostedion vitreum vitreum*. Also, nutrient requirements for striped bass, *Morone saxatilis*, (a coolwater or warmwater species depending upon the region of occurrence) are lacking except for protein requirements of the fingerling stage as a function of dietary lipid content (Millikin in press).

The present review provides an updated summary of qualitative and quantitative protein, amino acid, lipid, fatty acid, vitamin, and mineral requirements for all groups of fishes. Nutritive values of various feedstuffs, e.g., protein and lipid sources, and their relative contributions to cost-effective feed formulation, are not covered in this review.

Some topics important in fish nutrition that are not reviewed in the present article are metabolizable energy values of specific nutrients and feedstuffs for fishes and antinutritional factors often occurring in certain feedstuffs incorporated into commercial fish feeds. Metabolizable energy values of rainbow trout, *Salmo gairdneri*, have been examined for carbohydrates (Smith 1971), proteins (National Research Council 1981), and feedstuffs (Smith 1976; Smith et al. 1980; National Research Council 1981). Also, variability in heat increment as a portion of metabolizable energy resulting from protein, carbohydrate, or lipid ingestion was examined in rainbow trout and Atlantic salmon, *S. salar*, fingerlings (R. R. Smith et al. 1978). Important antinutritional factors often occurring in commercial-type diets for fishes are antitrypsin activity in soybeans (Sandholm et al. 1976), mycotoxins in peanut meal and cottonseed meal (Sinnhuber et al. 1977), gossypol in cottonseed meal (Ashley 1972), and cyclopropenoid fatty acids as cocarcinogens fed simultaneously with aflatoxins to rainbow trout (Sinnhuber et al. 1968). An informative review of antinutritional factors in fish feeds is included in a review of nutrient requirements of coldwater fishes (National Research Council 1981).

PROTEIN

Optimal dietary protein concentrations for fish are dictated by a delicate balance of dietary protein-to-energy ratio, plus protein quality (amino acid balance), and nonprotein energy sources (i.e., amount of fat in relation to carbohydrate). Excessive nonprotein energy intake resulting from high digestible energy-to-dietary-protein ratios often causes cessation of feeding before sufficient protein is consumed, since ingestion rate is primarily determined by total available dietary energy content (Page and Andrews 1973). Conversely, slow growth rates may result from low nonprotein energy intake or formula diets may simply be less cost-effective for fish farming purposes. Dietary protein in excess of that required for growth is often utilized for energy in fishes (Cowey 1979). For example, increased gluconeogenesis was demonstrated, as a result of higher activities of the gluconeogenic enzymes, fructose diphosphate, and phosphoenolpyruvate carboxykinase, in rainbow trout fed high dietary protein concentrations (Cowey et al. 1981b). Finally, dietary amino acid imbalances may result in higher dietary protein concentrations than that required for maximal growth as well as antagonisms between some amino acids, such as isoleucine and leucine in chinook salmon, *Oncorhynchus tshawytscha*, (Chance et al. 1964), isoleucine, leucine, and valine in channel catfish (Robinson et al. 1982), or lysine and arginine in salmonids (Rumsey[3]).

[3]Gary L. Rumsey, Tunison Laboratory of Fish Nutrition, U.S. Fish and Wildlife Service, Cortland, NY 13045, pers. commun. December 1981.

Since dietary protein quantity and quality are major determinants of growth in fish, numerous investigations have been conducted to determine protein requirements for specific fish species. Protein requirement studies that examine various concentrations of dietary protein with higher carbohydrate concentrations being substituted for protein in lower protein diets often produce reliable approximations of quantitative dietary protein requirements (Table 2). However, according to Rumsey (1978), protein sources generally have higher metabolizable energy values than carbohydrate sources for salmonids. Thus, in many dietary protein requirement studies, fishes were probably offered higher metabolizable energy values in the high protein diets compared with the low protein diets. Since fish fed low protein diets may have had less available energy, additional protein may have been shunted for metabolic requirements other than growth. Many of the quantitative protein requirements, listed in Table 2, may be overestimated values due to this shift in utilization of protein in low protein diets (Rumsey 1978). Therefore, protein-energy studies examining several energy concentrations within each of several dietary protein concentrations provide better estimates of quantitative dietary protein requirements of fishes.

Dietary protein concentration requirements generally decrease with increasing age or fish size. For example, salmonids require about 50% protein[4] during the initial feeding stage of fry, decreasing to 40% protein after 6 to 8 wk, with a further reduction to 35% protein for yearlings (National Research Council 1973). Channel catfish fry require a minimum of 40% protein, decreasing to 30 to 36% for fingerlings and 25 to 30% protein for subadults weighing >114 g (National Research Council 1977; Andrews 1977).

TABLE 2.—Quantitative protein requirements of several fish species.

Species	Initial mean weight	Protein requirement, % dry diet	Study duration (wk)	Rearing temperature (°C)	Criteria[1]	Reference
Salmo gairdneri	6.9	40	10	16-27	G,FC,BP	Satia (1974)
	1.3	45	10	10	G,FC	Halver et al. (1964)
	61.0	42	22	8-12	G,BP	Austreng and Refstie (1979)
	0.7	40	32	15	G,FC	Cho et al. (1976)
	6.5-7.0	[2]40-45	10	9-12.5	G,PER,FC	Zeitoun et al. (1973)
Oncorhynchus kisutch	14.5	40	10	6.5-10.5	G	Zeitoun et al. (1974)
O. tshawytscha	1.5	55	10	15	G	DeLong et al. (1958)
	1.5	40	10	8	G	DeLong et al. (1958)
O. nerka	1.15	45	10	10	G,FC	Halver et al. (1964)
Micropterus salmoides	?	40	2-8	23	G,FC	Anderson et al. (1981)
M. dolomieui	?	45	4-9	20.5	G,FC	Anderson et al. (1981)
Morone saxatilis	2.25	[3]55	6	24.5±2	G,FC	Millikin (1982)
	1.41	47	10	20.5	G,FC	Millikin (in press)
Pleuronectes platessa	14.5	50	12	15	G	Cowey et al. (1972)
Fugu rubripes	2.0	50	3	25-26	G,FC	Kanazawa et al. (1980b)
Anguilla japonica	3.1	44.5	8	25	G,BP	Nose and Arai (1972)
Tilapia zilli	1.65	35	3	24-26	G	Mazid et al. (1979)
T. aurea	0.4	[3]36	12	26-29	G	Davis and Stickney (1978)
Ictalurus punctatus	?	35	26	?	G,FC	Lovell (1972)
	10-25	35	8	28	G,PER	Murray et al. (1977)
Chanos chanos	0.04	40	4	25-28	G,FC	Lim et al. (1979)
Ctenopharyngodon idella	0.15-0.20	41-43	6	22-23	G,PER	Dabrowski (1977)
Cyprinus carpio	5.8	38	4	?	G	Ogino and Saito (1970)
Chrysophrys aurata	2.6	38	16	?	G,FC	Sabaut and Luquet (1973)

[1]G = growth, FC = feed conversion, BP = body protein, PER = protein efficiency ratio.
[2]Protein requirement increased from 40 to 45% as salinity increased from 10 to 20‰.
[3]Highest protein concentration examined.

The higher protein concentrations in these two ranges produce better growth of channel catfish fingerlings and subadults, whereas the lower protein concentrations provide better protein conversion (weight protein fed ÷ weight gain) (Andrews 1977).

Increased water temperature has variable effects on the minimal protein or energy requirement for maximal growth rate of fishes. For example, chinook salmon fingerlings require 40% protein at 8°C and 55% protein at 15°C (DeLong et al. 1958). Striped bass fingerlings (initial mean weight = 1.4 g) require 47% protein at 20.5°C, while additional dietary protein is required (about 55%) at 24.5°C for maximal growth of slightly larger fingerlings (initial mean

[4]Nutrient content of diets is expressed as percentage of the diet on a dry weight basis, unless otherwise noted.

weight = 2.2 g) (Millikin in press and 1982, respectively). In separate studies with rainbow trout fingerlings, 35% dietary protein provided as good a growth rate as 40 or 45% protein within any of several temperature regimes (National Research Council 1981). Fingerlings (mean initial weight = 2.0 g) fed either 35, 40, or 45% protein grew equally well within any one temperature regime (9°, 12°, 15°, and 18°C) over a 16-wk period (Slinger et al. 1977, cited in National Research Council 1981). Slightly larger rainbow trout (mean initial weight = 3.45 g) also grew equally well when fed 35, 40, or 45% dietary protein within any one of three temperature regimes (9°, 12°, or 18°C) over a 24-wk period (Cho and Slinger 1978, cited in National Research Council 1981). Growth rates were progressively higher at each successive increase in rearing temperature, regardless of dietary protein concentration, except for 18°C in the second study. Increased feed consumption of lower protein diets occurred when rainbow trout were reared at higher temperatures and probably satisfied higher protein requirements at elevated water temperatures (National Research Council 1981). Chinook salmon fry (0.4 g) require 53% dietary protein (dry weight basis) combined with 16% dietary lipid (dry weight basis) when reared at 5° or 12°C based upon weight gain and survival rates (Fowler 1980, 1981). However, growth rates were two to three times more rapid for chinook salmon fry reared at 12°C.

Changes in salinity may alter protein requirements of anadromous or euryhaline species. Rainbow trout fingerlings require 45% protein for optimal growth at 20‰ compared with a 40% protein requirement at 10‰ (Zeitoun et al. 1973). Since a salinity of 10‰ is almost isotonic with internal fluids (9‰) of rainbow trout fingerlings, the higher dietary protein requirement for rainbow trout reared in a salinity of 20‰ suggests that the higher dietary protein concentration may assist in osmoregulation in a hypertonic external environment for this species (Zeitoun et al. 1973). Conversely, coho salmon, *O. kisutch*, smolts require 40% protein in 10 and 20‰. Although maximum weight gain occurred at 40% protein in both salinities, maximum protein retention occurred at 40% protein in 10‰ and 50% protein at 20‰ (Zeitoun et al. 1974). The authors concluded that the hyperosmotic environment (20‰) did not stress coho salmon smolts in the same manner as previously shown with smaller rainbow trout fingerlings. Also, underyearling rainbow trout (mean weight = 70 g) require more dietary arginine (1.2% of the diet) when reared in freshwater than in those individuals reared in 20‰ (1.0% arginine of the diet) (Kaushik 1977, cited in Poston 1978). Further work is necessary to more firmly establish whether protein requirements change with salinity for specific life stages of various anadromous or catadromous fish species.

AMINO ACIDS

Qualitative and Quantitative Requirements

Examination of qualitative amino acid requirements of fishes has often been based upon growth and feed efficiency in long-term feeding studies. Typically, one of several amino acids is removed singly from a well-defined formula diet which is assumed to be nutritionally complete (i.e., positive control), to determine if significant reduction in weight gain occurs in fish fed the selected, amino acid-deficient diets compared with growth of fish fed the control diet. Thereafter, any group of fish fed a diet determined to be deficient in an amino acid, as indicated by reduced growth and feed efficiency, is separated into two subgroups: One subgroup is retained on the amino acid-deficient diet (control diet minus one amino acid), whereas the other subgroup is fed the control diet. Reduced growth rate or cessation of growth in fish fed the amino acid-deficient test diet versus the control diet is considered to be confirmation of a dietary requirement for the specific amino acid being tested. On the basis of such amino acid feeding studies, several fish species have been found to require the same 10 amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine) as essential dietary constituents. Species requiring dietary inclusion of these amino acids include chinook salmon (Halver et al. 1957); rainbow trout (Shanks et al. 1962); sockeye salmon, *O. nerka* (Halver and Shanks 1960); channel catfish (Dupree and Halver 1970); Japanese eel, *Anguilla japonica*, and European eel, *Anguilla anguilla* (Arai et al. 1972b); common carp (Nose et al. 1974); red sea bream, *Chrysophrys major* (Yone 1975); and redbelly tilapia, *Tilapia zilli* (Mazid et al. 1978).

Qualitative amino acid requirements of plaice, *Pleuronectes platessa*, and sole, *Solea solea*, were investigated, using intraperitoneal injections of uniformly labelled - ^{14}C-glucose into individuals

of the two fish species (Cowey et al. 1970). Formation of radioactive labelled aspartic acid, glutamic acid, cysteine, serine, glycine, alanine, and proline over a 6-d period implied that sufficient amounts of these amino acids can be produced by underyearling plaice and sole through intermediary metabolism, thus suggesting dietary nonessentiality of those specific amino acids. On the other hand, arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, and valine were not incorporated from (U-^{14}C)-glucose, thus implying dietary essentiality. Although the authors suggested that metabolic requirements for tyrosine were provided from hydroxylation of ingested phenylalanine, this still needs to be tested. Possible essentiality of tryptophan was not examined, thereby leaving the status of this amino acid unresolved for the plaice and sole.

Quantitative amino acid requirements determined for several fish species are generally based on weight gain, feed efficiency, and sometimes free amino acid plasma levels of individuals fed graded concentrations of a particular amino acid (Table 3). In addition to those values listed in Table 3, coho salmon have been shown to require 2.4% arginine of the dry diet (6.0% of the dietary protein), 0.7% histidine of the dry diet (1.7% of the dietary protein) (Klein and Halver 1970), and 0.2% tryptophan of the dry diet (0.5% of dietary protein) (Halver 1965). Many similarities exist between species in individual quantitative amino acid requirements when expressed as a percent of dietary protein (Table 3).

Amino acid composition of eggs and larval stages for a given species has been shown to be a good guideline for estimating quantitative amino acid requirements of fry and fingerling stages. For example, diets formulated to contain the amino acid composition of Atlantic salmon eggs promoted better growth of Atlantic salmon fingerlings than use of an amino acid pattern based on the National Research Council's (1973) recommendations for salmonids (Ketola 1980). Ketola (1980) also observed the same pattern of accelerated growth in rainbow trout fry fed diets formulated on the basis of egg amino acid composition of that species compared with the National Research Council's (1973) recommendations. In a separate study, rainbow trout fingerlings were fed a diet containing soybean meal as the sole protein source or the same diet supplemented with amino acids (leucine, methionine, lysine, valine, and threonine) to provide a dietary essential amino acid profile similar to rainbow trout eggs. Improved weight gain occurred in rainbow trout fingerlings fed the amino acid supplemented diet, thereby suggesting the similarity between amino acid profiles of rainbow trout eggs and dietary amino acid requirements of rainbow trout fingerlings (Rumsey and Ketola 1975).

Amino Acid Availability

A significant contribution to channel catfish diet formulation recently came from an extensive investigation of true amino acid availability (corrected for metabolic fecal amino acids) and apparent amino acid availability (digestibility) values of various feedstuffs commonly incorporated into commercial catfish diets (Wilson et al.

TABLE 3.—Quantitative dietary amino acid requirements for several fish species.[1]

Amino acid	Channel catfish[2]	Chinook salmon[3]	Japanese eel[4]	Common carp[5]
Arginine	4.3 (1.0)	6.0 (2.4)	4.5 (1.7)	4.2 (1.6)
Histidine	1.5 (0.4)	1.8 (0.7)	2.1 (0.8)	2.1 (0.8)
Isoleucine	2.6 (0.6)	2.2 (0.9)[6]	4.0 (1.5)	2.3 (0.9)
Leucine	3.5 (0.8)	3.9 (1.6)[6]	5.3 (2.0)	3.4 (1.3)
Lysine	5.1 (1.2)	5.0 (2.0)	5.3 (2.0)	5.7 (2.2)
Methionine	2.3 (0.6)[7]	4.0 (1.6)[8]	5.0 (1.9)[8]	3.1 (1.2)[9]
Phenylalanine	5.0 (1.2)[10]	5.1 (2.1)[6,11]	5.8 (2.2)[11]	6.5 (2.5)[11]
Threonine	2.3 (0.5)	2.2 (0.9)	4.0 (1.5)	3.9 (1.5)
Tryptophan	0.5 (0.1)	0.5 (0.2)	1.1 (0.4)	0.8 (0.3)
Valine	3.0 (0.7)	3.2 (1.3)	4.0 (1.5)	3.6 (1.4)

[1]Expressed as percentage of dietary protein with requirement as percentage of dry diet in parentheses.
[2]Based upon 24% dietary protein (Robinson et al. 1980a).
[3]Based upon 40% dietary protein unless otherwise noted (National Research Council 1973).
[4]Based upon 37.7% dietary protein (Nose and Arai Unpubl. data, cited in Cowey and Sargent 1979).
[5]Based upon 38.5% dietary protein (Nose 1979).
[6]Based upon 41% dietary protein (National Research Council 1973).
[7]In the absence of cystine which can replace 50 to 60% of methionine requirement (Harding et al. 1977).
[8]Methionine + cystine.
[9]In the absence of cystine.
[10]Phenylalanine + tyrosine requirement. Tyrosine can replace ca. 50% of phenylalanine (Robinson et al. 1980a).
[11]In the absence of tyrosine.

1981). Results generally suggested that reasonable agreement occurs between average apparent amino acid availability and protein digestibility values of any one specific protein source. However, individual amino acid availabilities were quite variable within and among various feed ingredients tested. Also, apparent amino acid availability values were considerably less than true amino acid availability values for feed ingredients containing relatively low protein content (e.g., 9 to 19%), such as rice bran, rice mill feed, wheat middlings, and corn.

Lysine

Dietary lysine requirements for fishes range from 5.0 to 6.8% of the dietary protein. In addition to the quantitative lysine requirements listed in Table 3, rainbow trout fry require 6.8% lysine and lake trout, *Salvelinus namaycush*, fry require 6.0% lysine as a percentage of total dietary protein (Ketola 1980). Robinson et al. (1980b) reported a dietary lysine requirement of 5% of the dietary protein for channel catfish fed an adequate dietary protein concentration (30%); thus confirming a dietary lysine requirement (5.1% of the dietary protein) for channel catfish fed a marginal dietary protein concentration of 24% (Wilson et al. 1977). Excessive dietary lysine in the presence of marginal or adequate dietary arginine concentrations did not depress growth or feed efficiency of channel catfish, nor did excessive arginine depress growth or feed efficiency of channel catfish in the presence of marginal dietary lysine concentrations (Robinson et al. 1981). This is in contrast to lysine-arginine antagonisms reported for several terrestrial species (Maynard and Loosli 1969).

Lysine deficiency in fish may conceivably result in depressed rates of collagen formation. Hydroxylysine has been shown to be a constituent of collagen in several fish species (Mehrle[5]). Fin rot occurred in rainbow trout fed a lysine-deficient diet containing corn gluten meal as the sole protein source (Ketola 1979a). Supplementation of a combination of lysine, arginine, histidine, isoleucine, threonine, tryptophan, and valine to the corn gluten meal diet resulted in improved survival, increased growth, and prevention of severe caudal fin erosion. At the same time, removal of lysine from the amino acid mixture in the corn gluten meal supplemented diet increased mortality, reduced growth, and resulted in caudal fin erosion of rainbow trout.

Methionine

Quantitative dietary methionine requirements for several fish species have been shown to depend upon dietary cystine concentration, since cystine can substitute for a portion of the methionine requirement. This is the result of the conversion of methionine to cystine being a common pathway of intermediary metabolism in many terrestrial animals (Maynard and Loosli 1969) as well as fish (National Research Council 1973). Rainbow trout fingerlings require 0.6% methionine (1.7% of the dietary protein) and 0.45% cystine (1.29% of the dietary protein), a total sulfur amino acid requirement of 1.05% of the diet (2.99% of dietary protein). This is based upon growth and feed efficiency as demonstrated by feeding studies, using a factorial design of 0.3 to 0.75% methionine and 0.04 to 0.6% cystine (Page 1978). Excessive cystine for rainbow trout (e.g., 0.6%) did not partially satisfy methionine requirements in methionine-deficient diets (0.3 and 0.45% methionine) based on weight gain and feed conversion. Chinook salmon require 0.5 to 0.6% dietary methionine (1.3 to 1.5% of the dietary protein) in the presence of 1.0% dietary cystine, whereas 1.6% methionine did not produce maximum growth in the presence of 0.05% dietary cystine (Halver et al. 1959). Channel catfish require 0.56% dietary methionine (2.34% of the dietary protein) in the absence of cystine, while 60% of the methionine requirement is replaceable with cystine (Harding et al. 1977).

Methionine deficiency has been shown to result in cataractogenesis in lake trout fingerlings and rainbow trout fingerlings. After 12 wk, rainbow trout fingerlings (initial mean weight = 1.5 g) fed 0.6% methionine plus 0.3 or 0.45% cystine did not develop any cataracts (Page 1978). Lower dietary methionine content (0.3 or 0.45%) combined with dietary cystine content ranging from 0.04 to 0.6% produced varying degrees of cataracts in rainbow trout. In another study, lake trout fingerlings were fed methionine-deficient diets (0.36% methionine = 0.96% of the dietary protein) containing soybean protein isolate as the sole protein source (40% of the diet). After 8 wk, lake trout fingerlings showed only initial signs of opacification of subcapsular areas (Pos-

[5]Paul M. Mehrle, Columbia National Fisheries Research Laboratory, U.S. Fish and Wildlife Service, Columbia, MO 65201, pers. commun. December 1981.

ton et al. 1977). However, after 16 wk, 100% of lake trout fed 0.36% dietary methionine developed bilateral lenticular cataracts, while none of the individuals fed the control diet containing 1.2% dietary methionine (3.27% of the dietary protein) had cataracts.

Attempts to supplement suboptimal dietary concentrations of methionine plus cystine with dietary taurine or inorganic sulfate have proven unsuccessful with channel catfish fingerlings and rainbow trout fingerlings. Channel catfish fingerlings fed dietary taurine or inorganic sulfate as a partial replacement for methionine had reduced growth rates (Robinson et al. 1978), whereas rainbow trout fingerlings had reduced growth and developed cataractogenesis (Page et al. 1978). The absence of cataractogenesis in methionine-deficient channel catfish may be the result of the relatively shorter duration of this study (8 wk) compared with a 16-wk study on lake trout (Poston et al. 1977). Another explanation for the absence of cataract formation in channel catfish may be due to the slightly larger initial size of channel catfish (mean weight = 7.7 g) compared with lake trout (mean weight = 5 g). Either of these factors may have produced a slower turnover rate of amino acids in channel catfish.

According to a summary by Poston et al. (1977), insufficient methionine often results in reductions in sulfhydryl group concentrations, and lens glutathione synthesis also decreases rapidly during formation of most cataracts. The authors speculated that lens glutathione possibly protects the lens sulfhydryl groups from oxidation.

Tryptophan

Tryptophan deficiency symptoms have been described in rainbow trout; sockeye salmon; brook trout, *S. fontinalis*; and channel catfish. Tryptophan deficiency in rainbow trout and sockeye salmon has resulted in scoliosis (Shanks et al. 1962; Halver and Shanks 1960, respectively). In a separate study with rainbow trout, hyperemia, scoliosis, and abnormal deposition of calcium occurred in kidney and bony plates surrounding the notochord and sheath of fish fed tryptophan-deficient diets (Kloppel and Post 1975). The authors suggested that hyperemia might be attributed to a lack of serotonin resulting from a deficiency of its precursor, tryptophan. In discussing scoliosis, Kloppel and Post (1975) noted that tryptophan is a major component of protocollagen, a supposed precursor of collagen. However, the absence of scoliosis in channel catfish fingerlings fed tryptophan-deficient diets (Wilson et al. 1978), compared with studies on salmonids, probably resulted from a slower growth rate of channel catfish because of a larger initial mean weight (12.5 g).

Quantitative tryptophan requirements have been shown to be similar for three different salmonid species and channel catfish. Almquist-type plots of growth responses indicated dietary tryptophan requirements of 0.15 to 0.25% of the diet (0.4 to 0.6% of dietary protein) for chinook salmon and 0.20 to 0.25% of the diet (0.5 to 0.6% of dietary protein) for sockeye salmon and coho salmon (Halver 1965). Channel catfish fingerlings fed a tryptophan-deficient diet (0.05%) for 8 wk had significantly poorer weight gain and feed efficiency than individuals fed diets containing as low as 0.12% tryptophan (0.5% of dietary protein) (Wilson et al. 1978). Wilson et al. (1978) suggested that the lower dietary tryptophan requirement of fishes compared with that of terrestrial animals may be due to an inability of fish to convert tryptophan to niacin, thus reducing the metabolic need of tryptophan in fishes as compared with terrestrial species. Growth rate of brook trout and the low ratio of two enzyme activities (3-hydroxyanthranilic acid oxygenase to picolinic acid carboxylase) concerned with an intermediate of the conversion pathway of tryptophan to niacin indicated that dietary tryptophan is not an efficient niacin precursor for this species (Poston and DiLorenzo 1973). Additionally, a low ratio of the two liver enzyme activities exists in lake trout, rainbow trout, Atlantic salmon, and coho salmon compared with terrestrial vertebrates (Poston and Combs 1980).

LIPIDS

Optimal Dietary Lipid Concentrations and Protein-to-Energy Ratios

Optimal dietary lipid concentrations for inclusion in formulated feeds for fishes involve consideration of several factors. The minimal dietary lipid concentration that maximizes dietary protein available for growth rather than energy (i.e., protein sparing) may be excessive for diet incorporation if fish are being cultured as a lean product for human consumption, or if freezer storage space is unavailable to retard develop-

ment of oxidative rancidity of the diets. However, if fish are being hatchery cultured for release into natural waters, high body lipid composition may be beneficial as an energy source during acclimation to natural food (Wedemeyer et al. 1980). Also, feeds that contain the minimal dietary lipid concentration required for maximal protein sparing action for a particular species are relatively cost-effective.

Protein sparing action of various dietary lipid concentrations has been examined for several fish species. Channel catfish fingerlings (mean initial weight = 1.25 g) cultured at 26.7° to 32.2°C and fed 35% protein diets grew faster on 8% dietary lipid, either as beef tallow or corn oil, than on 4% of either dietary lipid source (Dupree 1969a). Dietary lipid concentrations of 16% corn oil or beef tallow reduced growth rate and protein deposition of channel catfish compared with 8% dietary lipid. Therefore, maximal protein sparing action occurred at <16% of either dietary lipid source but ≥8% dietary lipid. In a separate study, larger channel catfish fingerlings (initial mean weight = 7.0 to 7.5 g), cultured at 30°C and fed 25% protein diets containing either 5, 8, 12, 15, or 20% bleached menhaden oil, had maximal weight gain and protein deposition when fed 25% protein with 15% lipid (Dupree et al. 1979). Channel catfish fingerlings (either 0.5 or 1.0 g initial mean weight in separate experiments) reared at 28°C grew faster when fed 35% protein plus 12% lipid, rather than 5% lipid combined with 25 or 35% protein or 12% lipid combined with 25% protein (Murray et al. 1977). Conversely, when channel catfish reared at 23°C were fed 25 or 35% protein combined with 5 or 12% lipid, 5% lipid plus 25 or 35% protein was sufficient for maximal weight gain and food conversion, probably due to lower metabolic requirements. Channel catfish with initial and final mean weights of 14 and 100 g, respectively, required 35% protein and 12% lipid, whereas subadults weighing 114 to 500 g required 25% protein and 12% lipid when reared at 27°C (Page and Andrews 1973). Protein-to-energy ratio requirements of channel catfish fingerlings (initial mean weight = 7.0 g) as a function of protein deposition were found to be 88 mg protein/kcal between dietary energy concentrations of 275 to 341 kcal/100 g when reared at 26.7°C (Garling and Wilson 1976). However, maximal weight gain occurred in fish fed 32 to 36% protein. Therefore, for the most cost-effective feed, the optimal dietary protein concentration for channel catfish fingerlings reared at 26.7°C is between 24 and 32%, when considering weight gain, feed efficiency, and protein deposition. Rainbow trout fingerlings (initial mean weight = 4.8 g) reared at 12.2°C over an 18-wk period had equally good growth rates when fed 35% protein and 24% lipid as individuals fed 44 or 53% protein, each combined with either 8, 16, or 24% lipid. This indicated a minimal dietary lipid concentration of 24% for maximal protein sparing action and an optimal protein-to-energy ratio of 73 mg protein/kcal (Lee and Putnam 1973). Conversely, a study evaluating three dietary protein concentrations (33, 39, and 44%) combined with 22% lipid in each of three forms (22% herring oil, 14.6% herring oil plus 7.4% lard, or 11% herring oil plus 11% lard) in a 3×3 factorial showed that better growth was obtained in rainbow trout fingerlings (initial mean weight = 5.4 g) fed 44% protein and 22% lipid, regardless of the ratio of herring oil to lard when reared at 11.5°C over a 14-wk period (Yu et al. 1977). Protein efficiency ratios and protein retention values were similar, regardless of dietary protein concentration and lipid source combinations fed to rainbow trout fingerlings. The contradictory results of these two studies in the minimal dietary protein required (35% protein plus 24% lipid versus 44% protein plus 22% lipid) for maximal growth of rainbow trout fingerlings can be partially explained by differences in dietary fiber concentrations. A low dietary fiber concentration (6.5%) was incorporated in diets containing 36, 44, or 53% protein plus 24% lipid, whereas a high dietary fiber concentration (22.4%) was incorporated in diets containing 36, 44, or 53% protein plus 8% lipid (Lee and Putnam 1973). However, in the study by Yu et al. (1977), dietary fiber concentrations were held constant at 11.2% in all diets. Therefore, variable dietary fiber concentrations in the first study may have differentially affected amino acid absorption rates or feed utilization. Successive increases in dietary lipid concentration of 7, 11, or 16% in 30% protein diets or 9, 15, or 21% lipid in 40% protein diets resulted in increased weight gain and improved feed conversion of rainbow trout fingerlings (initial mean weight = 2 g) within each dietary protein concentration when reared at 11°C (Reinitz et al. 1978b). Minimal dietary protein and lipid concentration requirements were not determined, since the highest dietary protein (40%) plus lipid (21%) combination that was evaluated also produced maximal growth and optimal feed conversion ratios for rainbow trout fin-

gerlings. A separate study demonstrated that about 35% protein combined with either 23 or 27% dietary lipid provided better growth of rainbow trout fingerlings than 36% dietary protein combined with 14% dietary lipid (Reinitz and Hitzel 1980). However, the two high lipid concentration diets did not produce better growth rates of rainbow trout fingerlings than a 35% protein, 18% lipid diet. C. E. Smith et al. (1979) reported that rainbow trout brood stock fed high energy, high protein diets (16% lipid plus 48% protein or 17% lipid plus 49% protein) produced a greater volume of larger eggs than did fish fed diets low and intermediate in energy and protein (6% lipid plus 36% protein or 9% lipid plus 42% protein). However, considerable variation in protein (i.e., amino acid profiles) and lipid (i.e., fatty acid profiles) sources used between diets in this study makes interpretation of the data difficult. Striped bass fingerlings reared at 20.5°C and fed 37, 47, or 57% protein with 7, 12, or 17% lipid in a 3×3 factorial design showed maximal protein sparing action of lipid for growth when fed 12% lipid combined with 47% dietary protein or 17% lipid combined with 57% protein (Millikin in press). Juvenile turbot, *Scophthalmus maximus*, fed 35% protein combined with 3, 6, or 9% lipid plus 9 or 18% carbohydrate attained best growth and feed conversion when fed the diet containing 35% protein, 9% carbohydrate, and 9% lipid (Adron et al. 1976). Possibly, additional dietary lipid would have further spared protein for growth rather than energy. Also, a diet containing 35% protein, 9% carbohydrate, and 9% lipid produced similar growth and feed conversion of turbot when compared with a diet containing 55% protein, 9% carbohydrate, and 3% lipid. Juvenile blue tilapia, *Tilapia aurea*, with initial and final mean weights of 2.5 and 7.5 g, respectively, require about 56% protein and 460 kcal/100 g diet (123 mg protein/kcal) while fish >7.5 g required 34% protein and 320 kcal/100 g diet (109 mg protein/kcal) for maximum growth (Winfree and Stickney 1981).

Essential Fatty Acids

Inclusion of either linolenic acid (18:3ω3) or a more highly unsaturated fatty acid in the ω3 series in the diet of rainbow trout is essential. Rainbow trout fingerlings fed diets containing 1% 18:3ω3 as a supplement to 7.8% corn oil doubled their weight gain compared with individuals fed 10% corn oil as the sole dietary lipid source (Lee et al. 1967). Castell et al. (1972a) determined that 1% 18:3ω3 or ethyl linolenate produced larger rainbow trout than 1% linoleic acid (18:2ω6) or ethyl linoleate. Additionally, 1% 18:3ω3 prevented essential fatty acid deficiency symptoms (e.g., fin erosion, heart myopathy, shock syndrome, and swollen, pale livers), while as much as 5% 18:2ω6 did not cure such symptoms (Castell et al. 1972b). Dietary linolenic acid's essentiality and growth enhancing ability for rainbow trout was confirmed in another study, wherein 1% methyl linolenate plus 4% methyl laurate (C 12:0) provided maximal growth and prevention of fatty acid deficiency symptoms compared with fish fed 5% methyl laurate (Watanabe et al. 1974). Rainbow trout fingerlings fed either 0.5% 20:5ω3 or 0.5% 22:6ω3 had better growth rates than individuals fed 0.5% 18:3ω3 in diets containing 5% total lipid, thereby showing a higher essential fatty acid efficiency of 20:5ω3 and 22:6ω3 at low dietary concentrations of these fatty acids (Takeuchi and Watanabe 1977). However, it is unknown whether evaluation of higher dietary concentrations (e.g., 1 to 3%) of each of these fatty acids would have produced similar differences in essential fatty acid efficiencies in terms of growth and feed efficiency of rainbow trout fingerlings. Yu and Sinnhuber (1972) found that 1% dietary 18:3ω3 or 1% docosahexaenoic acid (22:6ω3) provided similar growth rates in rainbow trout fingerlings. No higher dietary concentrations of either fatty acid were studied, nor were total dietary lipid concentrations >2% (dry diet basis) examined. The essentiality of 18:3ω3 for rainbow trout was further substantiated in a 34-mo feeding study in which fingerlings fed 1% ethyl linolenate plus 5% ethyl laurate grew to maturity and produced viable offspring which in turn had normal growth rates (Yu et al. 1979). Incorporation of 1.5% ethyl linoleate to a lipid mix of 1% ethyl linolenate plus 3.5% ethyl laurate did not confer any additional advantage in growth rate, percent fertile eggs, or percent viable fry for rainbow trout compared with individuals fed the 1% ethyl linolenate diet.

Closely related species such as coho salmon and rainbow trout have different quantitative dietary requirements for 18:3ω3 administered as the triacylglycerol, trilinolenin. Coho salmon fingerlings required 1 to 2.5% trilinolenin for maximum growth and feed efficiency when fed dietary trilinolenin concentrations ranging from 0 to 5%. High dietary trilinolein concentrations (>1%) in the presence of the optimal trilinolenin

concentrations fed to coho salmon fingerlings resulted in reduced growth rate and feed efficiency values (Yu and Sinnhuber 1979). On the other hand, rainbow trout fingerlings had best growth rates and feed efficiency when fed higher trilinolenin concentrations combined with low trilinolein concentrations (5% trilinolenin plus 0% trilinolein or 3% trilinolenin plus 1% trilinolein) (Yu and Sinnhuber 1976). In a separate study, rainbow trout fingerlings fed a diet sufficient in 18:3ω3 (1% ethyl linolenate) actually had better growth rates and feed efficiency than fish fed 1% ethyl linolenate plus 1.5% ethyl linoleate (Yu and Sinnhuber 1975). Dietary supplements of 5% ethyl linoleate to feeds containing 0.1, 0.5, or 1% ethyl linolenate markedly reduced growth and feed efficiency of rainbow trout fingerlings.

Chum salmon, *O. keta*, fed 5% dietary lipid as either 5% methyl laurate, 4% methyl laurate plus 1% 18:2ω6, 4% methyl laurate plus 1% 18:3ω3, or 3% methyl laurate plus 1% 18:2ω6 and 1% 18:3ω3, showed best weight gain and feed efficiency when offered the 3% methyl laurate plus simultaneous supplements of 1% 18:2ω6 and 1% 18:3ω3 (Takeuchi et al. 1979). Also, simultaneous supplementation of 18:2ω6 (1%) and 18:3ω3 (1%) produced slightly better weight gain of chum salmon fingerlings than 4% methyl laurate plus 1% of a highly unsaturated fatty acid mix (containing 26.5% 20:5ω3 plus 42.1% 22:6ω3). However, minimal dietary requirements of 18:2ω6 or 18:3ω3 for optimal growth rate of chum salmon fingerlings were not determined.

Dietary supplements of either methyl linoleate or methyl linolenate at 0.5 or 1.0% concentrations provided better growth of Japanese eel fingerlings than a fat-free diet or 7% methyl laurate (T. Takeuchi et al. 1980). However, contradictory results in two separate studies by these investigators prevent any conclusions regarding minimal requirements of 18:2ω6 and 18:3ω3 for this species.

Common carp fry and fingerlings have demonstrated better growth when fed diets containing highly polyunsaturated fats (e.g., cod liver oil) than those containing 5% methyl laurate (Watanabe 1975a, b). Intermediate growth rates occurred in common carp fry fed either 1% methyl linoleate or 1% methyl linolenate plus 4% methyl laurate over a 22-wk period (Watanabe et al. 1975a), whereas 1% methyl linoleate or 1% methyl linolenate did not improve growth of common carp fingerlings over an 18-wk period (Watanabe et al. 1975b).

High variability exists among various fish species in ability to elongate and desaturate dietary 18-carbon fatty acids to 20- or 22-carbon fatty acids. Several marine species appear to have lower enzymatic elongation-desaturation capabilities than freshwater fishes. Administration of (1 $-$ ^{14}C) 18:3ω3 to individuals of red sea bream; black sea bream, *Mylio macrocephalus*; opaleye, *Girella nigricans*; striped mullet, *Mugil cephalus*; and rainbow trout indicated that only rainbow trout exhibited appreciable radioactivity in 22:6ω3 of body lipids (Yamada et al. 1980). Therefore, it was concluded that marine species have limited ability to elongate and desaturate 18:3ω3, resulting in dietary essentiality of eicosapentaenoic acid (20:5ω3) or 22:6ω3 and nonessentiality of 18:3ω3. In another study, injections of (1 $-$ ^{14}C) 18:3ω3 into two individuals of each of several fish species resulted in intensive incorporation of 18:3ω3 into 20:5ω3 and 22:6ω3 in rainbow trout, while very low percent bioconversion of 18:3ω3 to 20:5ω3 and 22:6ω3 occurred in marine fish such as globefish, *Fugu rubripes rubripes*; Japanese eel; red sea bream; rockfish, *Sebasticus marmoratus*; and ayu, *Plecoglossus altivelis* (Kanazawa et al. 1979). The results of this study confirmed that pathways of elongation and desaturation of dietary 18-carbon fatty acids are poorly developed in marine fishes compared with rainbow trout. Earlier, Castell et al. (1972c) had reported elevated 20:4ω6 and 22:5ω6 concentrations in body lipids of rainbow trout fed 1% 18:2ω6 as well as elevated 22:6ω3 concentrations in individuals fed 1% 18:3ω3, suggesting an ability of rainbow trout to elongate and desaturate linoleic and linolenic acid. Also, rainbow trout, fed a fat-free diet or 5% oleic acid (18:1ω9) as the sole dietary lipid, accumulated high body lipid concentrations of eicosatrienoic acid (20:3ω9), an indicator of essential fatty acid deficiency in terrestrial animals. Furthermore, comparison of dietary fatty acid composition and initial and final body fatty acid composition of rainbow trout in another feeding study, suggests the ability of this species to elongate and desaturate 20:5ω3 into 22:6ω3 (Castledine and Buckley 1980). Cowey et al. (1976) concluded that turbot lack the necessary microsomal desaturases to effectively convert 18:1ω9, 18:2ω6, or 18:3ω3 into polyunsaturated fatty acids for deposition in neutral fats or phospholipids based upon growth and body lipid composition. Also, 1% dietary 18:3ω3 or 1% arachidonic acid (20:4ω6) in the pres-

ence of 4% 18:1ω9 promoted better growth of turbot than 1% 18:2ω6 plus 4% 18:1ω9. Additionally, 1% cod liver oil plus 4% 18:1ω9 produced better growth rates of turbot than all other dietary treatments (Cowey et al. 1976). Simultaneous supplementation of 0.45% 18:2ω6 and 0.45% 18:3ω3 as the only dietary constituents of the ω6 and ω3 series did not increase the level of 20:5ω3 or 22:6ω3 liver triglycerides in underyearling plaice (Owen et al. 1972). Growth studies of red sea bream indicated that a 2% dietary polyunsaturated fatty acid mix (38% 20:5ω3, 1.4% 22:5ω6, and 33.4% 22:6ω3) promoted significantly better weight gain than fish fed up to 4.2% dietary methyl linolenate (Fujii and Yone 1976). It was concluded that 18:3ω3 is not essential for red sea bream, since this species has little, if any, capability to elongate and desaturate 18-carbon fatty acids to 20- and 22-carbon fatty acids, based upon body fatty acid composition.

Specific qualitative and quantitative essential fatty acid requirements have not been determined for channel catfish fry (Yingst and Stickney 1979) and channel catfish fingerlings (National Research Council 1977; Stickney 1977). Nevertheless, growth rates of channel catfish in several studies comparing various lipid sources (e.g., beef tallow, menhaden oil, safflower oil, and corn oil) have consistently been high in individuals fed menhaden oil as the chief dietary lipid (Stickney and Andrews 1971, 1972; Murray et al. 1977; Dupree et al. 1979; Yingst and Stickney 1979, 1980). Typically, menhaden oil contains a large amount of fatty acids of the ω3 family (Stickney 1977), especially the polyunsaturated fatty acids (e.g., 3% 18:3ω3, 17% 20:5ω3, and 13% 22:6ω3). Therefore, ω3 fatty acids may be essential for channel catfish, especially in the fry and early fingerling stages.

Unlike most fish species studied, *Tilapia zilli*, fingerlings require 1% 18:2ω6 or 20:4ω6 for optimal weight gain as opposed to fatty acids of the ω3 series (Kanazawa et al. 1980a). However, this same species has a greater relative ability to elongate and desaturate 18:3ω3 to 20:5ω3 and 22:6ω3, than to elongate and desaturate 18:2ω6 to 20:4ω6 (Kanazawa, Teshima, and Imai 1980).

In a review of lipid requirements of fishes, Castell (1979) discussed differences in fatty acid composition of fishes due to salinity, temperature, diet composition, depth, seasonal variation, and reproductive stage; requirements, metabolism, and functions of dietary fatty acids for fishes are also discussed.

CARBOHYDRATES

Carbohydrates are included in formulated feeds for fish primarily as a low cost source of energy to spare dietary protein for growth rather than energy. Protein sparing action of dietary carbohydrate was demonstrated in brook trout fed marginal concentrations of dietary protein (28 or 32%) with optimal protein-to-calorie ratios of 75 mg protein/kcal (Ringrose 1971).

Maximal dietary carbohydrate concentrations that can be fed to fish without reducing growth rate depend upon whether the fish species is carnivorous, omnivorous, or herbivorous. For example, maximal dietary dextrin concentrations that did not reduce growth rate were 10% for yellowtail, *Seriola quinqueradiata*, 20% for red sea bream and 30% for common carp (Furuichi and Yone 1980). Rainbow trout subadults can be fed 38% wheat meal or 41% cooked wheat (17 to 25% of dietary metabolizable energy) without deleterious effects on growth (Edwards et al. 1977). Similarly, rainbow trout fed 32% wheat meal or 21% wheat meal plus 13% glucose (15 and 26% metabolizable energy of the diet) did not have significant differences in growth rate (Refstie and Austreng 1981). However, dietary Cerelose[6] concentrations as low as 14%, substantially increased liver glycogen concentrations of rainbow trout compared with fish fed 0 or 7% dietary Cerelose (Hilton 1982). Additionally, low rearing temperatures (10° vs. 15°C) for rainbow trout resulted in increased liver glycogen concentrations. Therefore, Hilton (1982) suggested that stocking rainbow trout with high liver glycogen concentrations into natural waters could result in impaired liver function. Incipient lethal levels of waterborne copper were reported to be lower for rainbow trout fed higher concentrations of available carbohydrate, probably as the result of impaired liver function from high liver glycogen content (Dixon and Hilton 1981).

Digestibility of carbohydrates is generally inversely related to molecular complexity. Thus, monosaccharides are more available nutritionally to fishes than are disaccharides,which in turn are more available than are polysaccharides. Relative growth rates of chinook salmon fingerlings fed 20% carbohydrate were as follows: glucose > sucrose > fructose > maltose > dextrin > potato starch > galactose (Buhler and

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

Halver 1961). Brook trout fingerlings (initial mean weight = 1.6 g) fed 14% glucose, galactose, or fructose over a 20-wk period had better growth rates when fed 14% glucose or fructose (McCartney 1971). Rainbow trout fingerlings had better growth rate, feed conversion, and protein efficiency when fed 30% glucose concentrations compared with 30% raw corn starch or 15% glucose plus 15% cellulose (Bergot 1979a). Dietary glucose concentrations as high as 30% doubled plasma glucose 6 h after the first meal, while normal plasma glucose concentrations were attained 24 h later (Bergot 1979b). Channel catfish fingerlings can utilize 2.25 g of dextrin in place of 1 g of lipid for growth equally well within dietary lipid concentrations of 5 to 12.5% and digestible carbohydrate concentrations of 5.6 to 22.5% (Garling and Wilson 1977).

Dietary fiber is not required by fishes and is considered to be a nonnutrient bulk component in fish diets. According to Leary and Lovell (1975), dietary cellulose in excessive amounts probably decreases absorption of essential nutrients by physical obstruction of enzymes and increased rate of passage through the digestive system. Obstruction of enzyme activity may result from ingested fiber chelating metal ions serving as cofactors of enzymes. Dietary cellulose concentrations as high as 8% did not inhibit growth of channel catfish, whereas 14% dietary cellulose depressed growth. No similar studies have been conducted with salmonids or other fish species to evaluate maximum tolerable, dietary fiber concentrations.

Cellulase activity in stomachs of several fish species and intestinal portions of stomachless Cyprinidae was positively correlated with amount of detritus consumed (Prejs and Blaszczyk 1977). Microflora ingested along with detrital material is probably responsible for the cellulase activity in fish; however, further research should examine sources of cellulase activity, especially in herbivorous species.

VITAMINS

Qualitative vitamin requirements of fishes (National Research Council 1973, 1977) and their biochemical and physiological functions are generally similar to requirements and functions demonstrated for terrestrial animals. Early qualitative vitamin requirement studies of fishes usually consisted of long-term feeding trials (e.g., 14 to 24 wk) in which laboratory cultured salmonids were fed a positive control diet (i.e., assumed to be nutritionally complete) or that same diet omitting one of several vitamins (McLaren et al. 1947; Halver and Coates 1957; Coates and Halver 1958). Growth, survival, behavior, internal organ appearance, blood physiology, and histopathology were often examined to describe deficiency symptoms. Also, fish fed a vitamin-deficient diet were often divided into two subgroups during the course of the study. One subgroup remained on the vitamin-deficient diet while the recovery subgroup was fed the complete diet to detect positive responses such as accelerated growth rate and disappearance of deficiency symptoms.

More recently, biochemical criteria such as activities of specific enzymes requiring a given vitamin for coenzyme formation have been used to determine qualitative and quantitative vitamin requirements of fishes (C. E. Smith et al. 1974; Cowey 1976). According to C. E. Smith et al. (1974), biochemical defects in the form of reduced enzyme activity allow detection of preclinical vitamin deficiencies. A review of vitamin requirements of fishes was presented by Halver (1979).

Thiamine

Essentiality of dietary thiamine has been verified for brook, brown (*Salmo trutta*), and rainbow trout (McLaren et al. 1947; Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a; Aoe et al. 1969), Japanese eel (Arai et al. 1972a), red sea bream (Yone 1975), and turbot (Cowey et al. 1975). Thiamine deficiency symptoms commonly observed in many of these fish species include anorexia, poor growth, depigmentation, and loss of equilibrium. Hemorrhage and congestion of fins has been noted in thiamine-deficient Japanese eel (Hashimoto et al. 1970; Arai et al. 1972a) and thiamine-deficient common carp (Aoe et al. 1969).

Quantitative thiamine requirements have been determined for turbot and channel catfish. Cowey et al. (1975) detected optimal erythrocyte transketolase (thiamine pyrophosphate serves as coenzyme) activity in turbot fed 2.6 mg thiamine/kg dry diet, whereas maximal growth occurred at dietary thiamine concentrations $\geq$0.6 mg/kg dry diet. Therefore, in addition to growth rates, functional evidence such as enzyme activity also

provides additional useful information for estimating quantitative vitamin requirements. Channel catfish fingerlings require a minimal dietary thiamine concentration of 1 mg/kg dry diet based upon maximal weight gain, feed efficiency, and prevention of thiamine deficiency symptoms such as anorexia, poor growth, dark coloration, and higher mortality (Murai and Andrews 1978a). Hematocrit values of channel catfish were unaffected by dietary thiamine concentrations ranging from 0.1 to 20.1 mg/kg dry diet.

It is unknown why channel catfish and common carp require lower dietary concentrations of thiamine compared with salmonids. Omnivorous fish would seemingly require higher amounts of thiamine for oxidative decarboxylation of pyruvate and the transketolase reaction of the pentose phosphate shunt, due to the ability of herbivores and omnivores to metabolize higher dietary carbohydrate concentrations than carnivorous fish such as salmonids (Murai and Andrews 1978a).

Riboflavin

Dietary essentiality for riboflavin has been reported for rainbow trout (McLaren et al. 1947), brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), Atlantic salmon (Phillips 1959a), channel catfish (Dupree 1966), common carp (Aoe et al. 1967a; Ogino 1967), rainbow trout (Kitamura et al. 1967a; Poston et al. 1977; L. Takeuchi et al. 1980), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Rainbow trout (mean initial weight = 5.9 g) fed riboflavin-deficient diets developed bilateral corneal and lenticular lesions after 11 and 15 wk of the experimental period (Poston et al. 1977). Further evaluations of cataract formations induced from riboflavin deficiency in rainbow trout fingerlings confirmed no retinal damage according to histopathological examinations (Hughes et al. 1981a). Fin necrosis, snout erosion, and spinal deformation also occurred in riboflavin-deficient rainbow trout (Poston et al. 1977). In a separate study, rainbow trout fingerlings (initial mean weight = 1.5 g) fed riboflavin-deficient diets displayed anorexia, poor growth, high mortality rate, lesion of fins, and cataract formation during an 8-wk study (L. Takeuchi et al. 1980). Common carp fingerlings fed riboflavin-deficient diets showed anorexia, poor growth, high mortality rate, and hemorrhage of skin and fins (L. Takeuchi et al. 1980). Murai and Andrews (1978b) reported 100% occurrence of "short body dwarfism" due to shortening of individual vertebrae in riboflavin-deficient channel catfish after 20 wk. These authors speculated that abnormal vertebral growth may be related to hypothyroidism which in turn may be caused by riboflavin deficiency.

Quantitative riboflavin requirements have been determined for common carp, rainbow trout, and channel catfish. In several different studies, riboflavin requirements of carp fingerlings apparently declined with increasing fish size based on growth rate and liver riboflavin content. Common carp fingerlings with an initial mean weight equalling 1.5 g required 20 mg riboflavin/kg dry diet over a 6-wk period (Aoe et al. 1967a). Slightly larger carp fingerlings (initial mean weight = 2.8 g) required 10 mg riboflavin/kg dry diet over a 6-wk period (Ogino 1967), whereas individuals with an initial mean weight equalling 3.4 g required 5 to 7 mg riboflavin/kg dry diet (L. Takeuchi et al. 1980). Rainbow trout with an initial mean weight of 7 g required 12.2 mg riboflavin/kg for maximal growth, whereas 18.2 mg riboflavin/kg were required for saturation of head and posterior kidney tissue (Woodward 1982). However, larger rainbow trout fingerlings (initial mean weight = 11.2 g) required 3 mg riboflavin/kg dry diet according to growth, food conversion, and mean erythrocyte glutathione reductase activity coefficient or 12 mg riboflavin/kg dry diet for maximal liver riboflavin content (Hughes et al. 1981b). Rainbow trout fingerlings (initial mean weight = 1.5 g) required 4 mg riboflavin/kg dry diet based upon growth rate and feed efficiency and 6 mg riboflavin/kg dry diet based on liver riboflavin content (L. Takeuchi et al. 1980). Channel catfish fingerlings require 9 mg riboflavin/kg dry diet for maximal growth and 3 mg riboflavin/kg dry diet to prevent occurrence of short body dwarfism (Murai and Andrews 1978b).

Pyridoxine

Dietary essentiality of pyridoxine has been reported for rainbow trout (McLaren et al. 1947), brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), Atlantic salmon (Phillips 1959a), coho salmon (Coates and Halver 1958), common carp (Ogino 1965), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), yellowtail (Sakaguchi et

al. 1969), Japanese eel (Arai et al. 1972a), red sea bream (Yone 1975), turbot (Adron et al. 1978), and gilthead bream, *Sparus aurata* (Kissil et al. 1981). Coates and Halver (1958) mentioned several pyridoxine deficiency symptoms for coho salmon including nervous disorders, hyperirritability, poor appetite, indifference to light, and rapid occurrence of postmortem rigor mortis. Halver (1957) reported the following additional pyridoxine deficiency symptoms for chinook salmon: ataxia, edema of peritoneal cavity, colorless serous fluid, blue-green coloration on dorsal surface, and excessive flexing of opercles. Clinical signs of pyridoxine deficiency in rainbow trout include hyperirritability, nervous disorders, erratic and rapid swimming, flexing of opercles, greenish-blue coloration, and tetany, just before death (C. E. Smith et al. 1974). Pyridoxine-deficient rainbow trout displayed normocytic, normochromic anemia, indicating that pyridoxine has a function in maintenance of normal erythropoiesis in this species (C. E. Smith et al. 1974). Also, rainbow trout fed pyridoxine-deficient diets for 7 d had lower aspartate aminotransferase activity in white muscle, whereas liver aspartate and alanine aminotransferase activity was reduced after 28 d (Jurss 1978, 1981). Pyridoxine deficiency symptoms in channel catfish fingerlings included nervous disorders, erratic swimming, opercle extension, and tetany (Dupree 1966). Andrews and Murai (1979) confirmed a pyridoxine requirement for channel catfish fingerlings, reporting that fish fed pyridoxine-deficient diets displayed anorexia, nervous disorders, tetany, and blue-green coloration on the dorsal surface. No anemia was detected in pyridoxine-deficient individuals, whereas a microcytic, normochromic anemia was observed in channel catfish fed 20 mg/kg or greater of pyridoxine. Chinook salmon fingerlings fed a high protein diet (65%) require about 15 mg pyridoxine/kg diet for optimal growth and disease resistance to *Vibrio anguillarum* (Hardy et al. 1979).

Quantitative pyridoxine requirements are known for channel catfish, red sea bream, gilthead bream, turbot, and common carp. Channel catfish fingerlings require a minimum of 4.2 mg pyridoxine/kg dry diet for maximal growth (Andrews and Murai 1979). Red sea bream required a minimum of 5 to 6 mg pyridoxine/kg dry diet for maximal glutamic oxaloacetic transaminase activity and maximal glutamic pyruvate transaminase activity (Yone 1975). A minimum of 2 to 5 mg pyridoxine/kg dry diet is required for maximal weight gain and pyridoxine liver content of red sea bream (Yone 1975). Kissil et al. (1981) reported optimal dietary pyridoxine concentrations for gilthead bream as a function of growth (1.97 mg pyridoxine/kg dry diet) and liver alanine aminotransferase activity (3.0 to 5.1 mg pyridoxine/kg dry diet). Pyridoxine deficiency symptoms in gilthead bream included hyperirritability, erratic swimming behavior, poor food conversion, retarded growth, and high mortality. Turbot fed pyridoxine concentrations of 1.0 mg/kg dry diet up to 30 mg/kg had similar growth rates, whereas individuals fed 0.26 or 0.50 mg pyridoxine/kg dry diet had reduced weight gain (Adron et al. 1978). Liver alanine aminotransferase activity and muscle and liver aspartate aminotransferase activity increased with higher dietary pyridoxine concentrations up to 2.5 mg/kg dry diet. Therefore, a dietary pyridoxine concentration of 2.5 mg/kg dry diet satisfied both maximal growth and liver aspartate aminotransferase activity for turbot. Common carp fingerlings required 5.4 mg pyridoxine/kg dry diet for maximal growth rate and prevention of deficiency symptoms (Ogino 1965).

Niacin

Niacin has been shown to be an essential dietary constituent for rainbow trout (McLaren et al. 1947), brook and brown trout (Phillips and Brockway 1957), lake trout (Phillips 1959b), chinook salmon (Halver 1957), channel catfish (Dupree 1966), common carp (Aoe et al. 1967c), Japanese eel (Arai et al. 1972a), brook trout (Poston and DiLorenzo 1973), and red sea bream (Yone 1975). Hemorrhage and lesions of the skin have been reported in niacin-deficient channel catfish (Andrews and Murai 1978) and Japanese eel (Arai et al. 1972a). Dietary requirements for maximal growth include 28 mg niacin/kg dry diet for common carp (Aoe et al. 1967c) and 14.4 mg niacin/kg dry diet for channel catfish fingerlings (Andrews and Murai 1978).

Pantothenic Acid

Essentiality of dietary pantothenic acid has been demonstrated for rainbow trout (McLaren et al. 1947), brown, brook, rainbow, and lake trout (Phillips and Brockway 1957), Atlantic salmon (Phillips 1959a), chinook salmon (Halver

1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Most of these species fed pantothenic acid-deficient diets displayed mucous covered gills, anorexia, reduced weight gain, and "clubbed gills."

Quantitative pantothenic acid requirements have been determined for channel catfish fry (250 mg/kg dry diet) and channel catfish fingerlings (10 mg/kg dry diet) (Murai and Andrews 1975 and 1979, respectively) and common carp fingerlings (40 mg/kg dry diet) (Ogino 1967). Murai and Andrews (1975) suggested that the relatively high dietary pantothenic acid requirements of channel catfish fry might be partially due to higher rates of micronutrient losses in small feed crumbles (high surface to volume ratio) fed to fry compared with larger feed particles fed to fingerlings.

Ascorbic Acid

Ascorbic acid has several important physiological functions in fishes and is the vitamin most sensitive to processing and storage losses in fish formula feeds. Therefore, extensive research has been conducted on qualitative and quantitative ascorbic acid requirements for fishes. Ascorbic acid is a cofactor of an enzyme which is involved in hydroxylation of proline and lysine during collagen formation, thereby contributing to bone and skin formation. Ascorbic acid also has a role in iron metabolism and detoxification of organic pollutants such as toxaphene and polychlorinated biphenyls during accumulation in the liver.

Qualitative dietary ascorbic acid requirements have been reported for rainbow trout (McLaren et al. 1947; Kitamura et al. 1965; Hilton et al. 1978; Sato et al. 1978; John et al. 1979), brook trout (Poston 1967), coho salmon and rainbow trout (Halver et al. 1969), yellowtail (Sakaguchi et al. 1969), Japanese eel (Arai et al. 1972a), channel catfish (Lovell 1973; Wilson and Poe 1973), red sea bream (Yone 1975), mrigal, *Cirrhina mrigala* (Mahajan and Agrawal 1980a), and snake head, *Channa punctatus* (Mahajan and Agrawal 1979). Ascorbic acid deficiency symptoms in coho salmon and rainbow trout include reduced growth, distorted and twisted filament cartilage of the gill arches, acute lordosis and scoliosis, and eventual dislocation of vertebrae (Halver et al. 1969). Other physiological changes in ascorbic acid-deficient rainbow trout include low hematocrit values (Hilton et al. 1978; John et al. 1979), and high plasma levels of triglycerides and cholesterol (John et al. 1979). Halver (1972b) reported that the rate of repair of experimentally induced wounds in salmonids is directly related to the amount of ascorbic acid intake. Rainbow trout fed ascorbic acid-deficient diets for 18 wk displayed impaired collagen formation in the skin according to an in vitro radioisotopic method with labeled proline (Yoshinaka et al. 1978). Brook trout fingerlings fed ascorbic acid-deficient diets over a 34-wk period developed scoliosis and/or lordosis, increased mortality rate, and internal hemorrhaging (Poston 1967). Scorbutic channel catfish experienced lordosis, scoliosis (and ultimately, broken back), hemorrhage within the vertebral column, and brittle vertebrae (Wilson and Poe 1973). Also, these investigators reported reduced serum alkaline phosphatase activity (65% lower), lower vertebral collagen content (42% less on a dry basis), and less hydroxyproline in the collagen of scorbutic channel catfish. Wilson and Poe (1973) speculated that reduced serum alkaline phosphatase activity may indicate reduced bone formation from lower osteoblastic activity. In addition to the aforementioned common ascorbic acid deficiency symptoms (e.g., lordosis, scoliosis, hemorrhage along spinal column, and poor growth), channel catfish had increased susceptibility to pathogenic bacterial infestation (*Aeromonas liquefaciens*) and occasional formation of hemivertebrae (Lovell 1973). Also, Halver et al. (1975) reported hyperplasia of nuclei of eye support cartilage in salmonids deficient in ascorbic acid. Vertebral collagen percentages of 24.5% or less and liver ascorbic acid concentrations of 50 μg/g or less occurred in ascorbic acid deficient channel catfish fingerlings with an initial mean weight equalling 22 g (Lovell and Lim 1978). In contrast, channel catfish fingerlings fed sufficient ascorbic acid had 26% or greater vertebral collagen and 65 μg or greater ascorbic acid/g of liver tissue. In a separate study, Lim and Lovell (1978) reported the following ascorbic acid deficiency symptoms in smaller channel catfish fingerlings (initial mean weight = 2.3 g): 1) anorexia after 9 wk, 2) scoliosis, lordosis, and darker pigmentation after 10 wk, and 3) lower hematocrit values after 18 wk. Also, liver ascorbic acid concentrations of 30 μg/g and vertebral collagen percentages of 25% or less occurred in ascorbic acid-deficient channel catfish in this smaller size range. Snake heads with

ascorbic acid deficiency had an elevated liver cholesterol content after 150 d, in addition to the occurrence of scoliosis, lordosis, and decreased ascorbic acid concentrations in blood and kidney (Mahajan and Agrawal 1979). Ascorbic acid deficiency in fish from the same study resulted in normochromic, normocytic anemia after 120 d and normochromic, macrocytic anemia between 180 and 210 d (Agrawal and Mahajan 1980). Using ^{45}Ca as a tracer, snake heads had reduced absorption of calcium from surrounding water by gills and skin and lower muscle and bone calcium content when fed an ascorbic acid-deficient diet for 210 d (Mahajan and Agrawal 1980b). Since distortion of gill filaments from cartilage malformation often occurs in ascorbic acid-deficent fish, decreased calcium absorption through the gills may have resulted from the ascorbic acid deficiency (Mahajan and Agrawal 1980b). Channel catfish (initial weight slightly >5 g), fed either 670 or 5,000 mg of ascorbic acid/kg dry diet, did not receive any additional advantages in weight gain or backbone collagen concentration (Mayer et al. 1978). However, channel catfish exposed to increasingly higher concentrations of toxaphene were at least partially protected from growth retardation, vertebral development anomalies, and skin integrity problems, when higher dietary ascorbic acid concentrations were consumed. For instance, the no-effect toxaphene concentration on skin integrity (e.g., mucous cell numbers and epidermal thickness) was <37 ng/l for channel catfish fed 63 or 670 mg ascorbic acid/kg dry diet, while the no-effect toxaphene concentration was between 68 and 108 ng/l for fish fed 5,000 mg ascorbic acid/kg dry diet (Mayer et al. 1978). Methods to measure rupture (the force level causing specimen failure) and elastic limit (the force level above which permanent structural damage occurs in a test specimen) according to Hamilton et al. (1981a) were used to evaluate effects of ascorbic acid deficiency on bone strength of channel catfish (Hamilton et al. 1981b). Channel catfish fingerlings (initial weight = 4 to 5 g) fed diets containing no ascorbic acid had significant reductions in length and weight after 150 d. Also, after 150 d, fish fed no supplemental ascorbic acid had reductions of 10% in backbone collagen and 16% in hydroxyproline concentration in collagen. Additionally, in channel catfish fed no supplemental ascorbic acid, 24% less force was required to cause permanent damage of vertebral centra (elastic limit) and failure of vertebral centra (rupture) occurred at 16% less force than in individuals fed 500 mg ascorbic acid/kg dry diet.

Quantitative ascorbic acid requirements have been determined for several fish species. Rainbow trout (initial mean weight = 0.3 g) require 100 mg ascorbic acid/kg dry diet and coho salmon (initial mean weight = 0.4 g) require about 50 mg ascorbic acid/kg dry diet based upon blood and anterior kidney ascorbic acid concentrations and growth rate (Halver et al. 1969). The minimal level of ascorbic acid in the blood of coho salmon and rainbow trout accompanying normal growth and survival rate is 35 μg ascorbic acid/g blood. Hilton et al. (1978) reported a lower ascorbic acid requirement (40 mg/kg dry diet) for larger rainbow trout (initial mean weight = 6.7 g), based upon growth, feed conversion, survival rate, and serum iron levels. Andrews and Murai (1975) estimated that channel catfish fingerlings (initial mean weight = 2.3 g) require 50 mg ascorbic acid/kg dry diet over a 28-wk period based on growth, feed conversion, and absence of ascorbic acid deficiency symptoms. Channel catfish fingerlings (initial mean weight = 2.3 g) required 30 mg ascorbic acid/kg dry diet over a 22-wk period for maximal growth, whereas 60 mg ascorbic acid/kg (the next highest experimental concentration) was sufficient to prevent distortion of gill filament cartilage and promote regeneration of skin and muscle in experimentally inflicted wounds after 10 d (Lim and Lovell 1978). Mahajan and Agrawal (1980a) concluded that mrigal fry and fingerlings require about 700 mg ascorbic acid/kg dry diet based upon growth, survival rates, and percentage occurrence of skeletal deformities.

Several sources of dietary ascorbic acid have been evaluated for relative nutritional value for channel catfish and rainbow trout. Channel catfish fingerlings (initial mean weight = 7.9 g) fed equimolar concentrations of 25 mg L-ascorbic acid (uncoated or ethylcellulose coated) or dipotassium L-ascorbate 2-sulfate dihydrate (AS) per kg dry diet over a 20-wk period did not show scoliosis, whereas 42% of the fingerlings fed a diet containing <5 mg ascorbic acid/kg dry diet had scoliosis (Murai et al. 1978). Maximal weight gains and feed efficiency of channel catfish varied with dietary ascorbic acid sources. Only 50 mg of ethylcellulose coated or uncoated L-ascorbic acid were required for maximal growth and feed efficiency, while 200 mg of L-ascorbate-2-sulfate dihydrate were required for similar increments of weight gain. Generally, growth

reached a maximum when blood L-ascorbic acid concentrations reached 7 μg/ml (Murai et al. 1978). Rainbow trout which were considerably younger (0.3 g) than channel catfish from the previous study, required about 80 mg of dipotassium ascorbic-2-sulfate (DAS)/kg dry diet over a 20-wk period to avoid ascorbic acid deficiency symptoms in the majority of fishes, and 160 mg DAS/kg dry diet to achieve normal growth (Halver et al. 1975).

Choline

Dietary essentiality of choline has been demonstrated for rainbow trout (McLaren et al. 1947), brook and brown trout (Phillips and Brockway 1957), lake trout (Phillips 1959b), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967a), common carp (Ogino et al. 1970a), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). Choline deficiency symptoms in fish include poor growth and feed efficiency, anorexia, fatty livers, and hemorrhagic areas in kidneys, liver, and intestine.

Quantitative choline requirements have been estimated for common carp fingerlings and lake trout fingerlings. Ketola (1976) examined relative growth rates of lake trout fed an unsupplemented diet (30 mg choline/kg dry diet) compared with equimolar supplements of aminoethanol, dimethylaminoethanol, methylaminoethanol, betaine·HCl, and choline (equivalent to 2,600 mg choline/kg dry diet). Lake trout fed the unsupplemented diet and aminoethanol and betaine supplements had reduced growth rates and high liver fat content. It was concluded that since betaine, a source of labile methyl groups, did not affect growth or liver fat content, any metabolic function of choline in regulation of liver fat in lake trout is unrelated to transmethylation. In a separate feeding study, a quantitative dietary choline requirement of 1,000 mg/kg dry diet was determined for lake trout fingerlings (Ketola 1976). Common carp require an estimated minimal dietary choline·Cl concentration of 2,000 mg/kg dry diet based upon slightly reduced growth and fatty livers in individuals fed choline-deficient diets (Ogino et al. 1970a). The possible role of methionine as a methyl donor and its relative efficiency in preventing fatty liver and hemorrhagic degenerations of kidneys of choline-deficient fish has not yet been investigated.

Folic Acid and Cyanocobalamin

Qualitative folic acid requirements have been demonstrated for brook, brown, and rainbow trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), channel catfish (Dupree 1966), rainbow trout (McLaren et al. 1947; Kitamura et al. 1967a), Japanese eel (Arai et al. 1972a), and rohu, *Labeo rohita* (John and Mahajan 1979). However, common carp fingerlings (mean initial weight = 2.5 g) fed several folic acid concentrations (0 to 15 mg/kg diet) over 16 wk did not show differential responses in growth, feed conversion, folic acid liver content, and erythrocyte counts (Aoe et al. 1967b).

Folic acid deficiency symptoms in chinook salmon include poor growth, anorexia, anemia, lethargy, dark coloration, and megaloblastic erythropoiesis (Halver 1957), while coho salmon displayed poor growth and anorexia (Coates and Halver 1958). Channel catfish fed folic acid-deficient diets displayed lethargy, anorexia, and increased mortality (Dupree 1966). Anemia in coho salmon fed folic acid-deficient diets was macrocytic with poikilocytosis of erythrocytes and a reduction in number of the erythrocytes (Smith and Halver 1969). Clinical folic acid deficiency symptoms in coho salmon in the same study included reduced growth, pale gills, exophthalmia, dark coloration, and distended abdomens with ascites fluid. These authors suggested that blood cell formation in fish is very sensitive to folic acid deficiency because of the importance of folic acid in incorporation of nucleotides into deoxyribonucleic acid. Phillips (1963) detected anemia (type was not reported) in brook trout fingerlings fed folic acid-deficient diets after 9 wk.

Qualitative cyanocobalamin requirements have been demonstrated for chinook salmon (Halver 1957) and channel catfish (Dupree 1966). Halver (1957) reported growth retardation and reduced hemoglobin concentrations and erythrocyte numbers in chinook salmon fed a cyanocobalamin-deficient diet for 16 wk. Channel catfish fed cyanocobalamin-deficient diets displayed growth retardation after 36 wk (Dupree 1966) or lower hematocrits after 24 wk (Limsuwan and Lovell 1981). Limsuwan and Lovell (1981) demonstrated that intestinal microorganisms synthesized about 1.4 ng of cyanocobalamin/g body weight per day. Lack of differences in growth, hemoglobin concentration, and erythrocyte numbers in fish fed either 21.8 ng cyanocobalamin/g

diet or 1.8 ng cyanocobalamin/g diet suggested that cyanocobalamin requirements are marginal for channel catfish (initial mean weight = 7.1 g) over a 24-wk period. However, channel catfish fry and early fingerling stages may have demonstrated a cyanocobalamin requirement under similar conditions.

The effects of feeding folic acid-deficient or folic acid plus vitamin B_{12} (cyanocobalamin)-deficient diets have been examined with brook trout (Phillips 1963) and rohu (John and Mahajan 1979). During the time interval between 9 and 15 wk of a feeding study, anemia was more pronounced in brook trout fed a diet deficient in both vitamin B_{12} and folic acid than in individuals fed a diet deficient in folic acid only. Lethargy, muscular loss, and poor growth rate were accentuated in rohu fed a diet concurrently deficient in folic acid and cyanocobalamin, compared with fish fed diets deficient in either folic acid or cyanocobalamin, singly. Megaloblastic anemia occurred in rohu fed a folic acid-deficient diet, a cyanocobalamin-deficient diet, and a diet deficient in both vitamins (John and Mahajan 1979).

Biotin

Qualitative dietary requirements for biotin have been demonstrated for brook, brown, and lake trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), goldfish, *Carassius auratus* (Tomiyama and Ohba 1967), common carp (Ogino et al. 1970b), Japanese eel (Arai et al. 1972a), channel catfish (Robinson and Lovell 1978), and lake trout (Poston and Page 1982). Biotin deficiency symptoms generally occurring in salmonids include anorexia, poor growth, and depressed liver acetyl CoA carboxylase and pyruvate carboxylase (Poston and Page 1982). Biotin deficiency signs include spastic convulsions, fragmentation of erythrocytes, and muscle atrophy in chinook salmon (Halver 1957), depigmentation in channel catfish (Robinson and Lovell 1978), abnormal synthesis of liver fatty acids and high liver glycogen content in brook trout (Poston and McCartney 1974), pale-colored gills often with a mucous coating, protruding beyond the operculum in rainbow trout (Castledine et al. 1978), and high rates of deposition of glycogen in kidney tubules and short, thick gill lamellae in lake trout (Poston and Page 1982).

Biotin has been shown to be important in affecting growth and acetyl CoA carboxylase activity in fish. Lake trout fingerlings required a minimum of 0.1 mg biotin/kg dry diet for optimal growth rate and a minimum of 0.5 mg biotin/kg dry diet for optimal swimming stamina (Poston 1976a). Acetyl coenzyme A carboxylase activity has been shown to be fully activated in livers of rainbow trout containing >3.3 μg biotin/g liver (Castledine et al. 1978). Dietary biotin concentrations of 8 mg/kg dry diet enhanced liver pyruvate decarboxylase activity in channel catfish fingerlings (Robinson and Lovell 1978), whereas 6 mg biotin/kg dry diet increased acetyl CoA carboxylase and pyruvate decarboxylase activities in brook trout fingerlings (Poston and McCartney 1974). Common carp fingerlings require 1 mg biotin/kg dry diet for maximal weight gain and biotin liver content (Ogino et al. 1970b).

Since biotin-containing lipogenic and gluconeogenic enzymes or both may have low activity in biotin-deficient trout, increased liver glycogen concentrations and altered liver fatty acid compositions may result (Poston and McCartney 1974; Poston 1976a). High concentrations of liver glycogen were reported in biotin-deficient lake trout (Poston 1976a; Poston and Page 1982) and rainbow trout (Castledine et al. 1978). Altered liver fatty acid composition occurred in biotin-deficient brook trout (Poston and McCartney 1974) and rainbow trout (Castledine et al. 1978). Liver lipid concentrations did not vary between channel catfish fed 0% or 8 mg biotin/kg dry diet over a 22-wk period (Robinson and Lovell 1978). Biotin-deficient diets resulted in larger liver size in brook trout compared with individuals fed sufficient dietary biotin (6 mg/kg dry diet) (Poston and McCartney 1974), whereas the presence (8 mg/kg dry diet) or absence of dietary biotin did not affect liver size in channel catfish (Robinson and Lovell 1978).

Inositol

Qualitative requirements for inositol have been reported for rainbow trout (McLaren et al. 1947), brook, brown, and rainbow trout (Phillips and Brockway 1957), chinook salmon (Halver 1957), coho salmon (Coates and Halver 1958), common carp (Aoe and Masuda 1967), Japanese eel (Arai et al. 1972a), and red sea bream (Yone 1975). General inositol deficiency symptoms include poor feed digestibility and utilization, anorexia, reduced growth, and distended abdomens (Halver 1972a). Skin lesions occurred in common carp fed inositol-deficient diets and in-

cluded the following physiological and morphological changes: hemorrhage around the base of the dorsal fin, loss of skin mucosa, and "sloughing off" of scales and fins (Aoe and Masuda 1967).

Quantitative inositol requirements are available only for common carp and red sea bream. Common carp require 4 g inositol/kg dry diet for maximal weight gain, feed conversion, and prevention of skin lesions (Aoe and Masuda 1967). Red sea bream require between 550 and 900 mg inositol/kg dry diet in direct proportion to dietary glucose concentrations of 10 to 40% (Yone 1975). Currently, quantitative inositol requirements for salmonids are based upon dietary concentrations (250 to 400 mg/kg dry diet) that were included in the control diets used to determine qualitative vitamin requirements of chinook salmon (Halver 1957).

Vitamin A

Vitamin A has been shown to be an essential dietary constituent for channel catfish (Dupree 1966), rainbow trout (Kitamura et al. 1967b), common carp (Aoe et al. 1968), goldfish (Jones et al. 1971), and brook trout (Poston et al. 1977). General physiological functions of vitamin A in fish include a role in maintaining normal growth rate, pigmentation, and vision. Long-term feeding studies have consistently yielded various eye malformations (e.g., popeye, cataracts, hermorrhage) in fish fed vitamin A-deficient diets. Rainbow trout fed no supplemental vitamin A in a semipurified diet developed corneal pitting and homogeneous clouding, thickening of the corneal epithelium, and degeneration of the retina (Poston et al. 1977). However, growth during the 22-wk period was similar regardless of dietary vitamin A content (0% vs. 10,000 International Units (IU) vitamin A/kg dry diet). Brook trout of a smaller initial weight (0.15 g) than the rainbow trout fingerlings (5.9 g) grew significantly faster over a 20-wk period when fed 10,000 IU vitamin A/kg dry diet compared with 0% vitamin A (Poston et al. 1977). Pronounced eyeball protrusions and dermal depigmentation occurred in brook trout fed vitamin A-deficient diets. Histopathological examinations of eyes of salmonids have shown that lens damage does not occur in vitamin A-deficient fish (Poston et al. 1977). Vitamin A deficiency symptoms in channel catfish include depigmentation, opaque and protruding eyes, atrophy, and death (Dupree 1970). Vitamin A-deficient goldfish developed exophthalmos, loss of scales, anorexia, and eventual mortality (Jones et al. 1971).

Conversion efficiency of β-carotene to vitamin A has been examined indirectly for channel catfish and brook trout. Dupree (1966) indicated that 12 mg β-carotene/kg dry diet (equal to 20,000 IU of vitamin A/kg dry diet) were insufficient to prevent popeye in channel catfish fed vitamin A-deficient diets, whereas 450 IU of vitamin A/kg dry diet were sufficient to prevent occurrence of popeye in channel catfish fed diets devoid of β-carotene. These results suggested an inefficient conversion rate (if any) of β-carotene to vitamin A in channel catfish (Dupree 1966). In a separate study, channel catfish fingerlings (mean initial weight = 2.25 g) fed 1,000 IU vitamin A acetate had optimal weight gain and no occurrence of popeye or other vitamin A deficiency symptoms (Dupree 1970). Poston et al. (1977) demonstrated indirectly that brook trout can convert dietary β-carotene into vitamin A with conversion efficiency being greater at 12.4°C than at 9°C. Individuals fed 6 mg β-carotene/kg dry diet (10,000 IU vitamin A activity/kg for many terrestrial animals) without supplemental vitamin A did not develop depigmentation or pronounced eyeball protrusion. However, brook trout fed 10,000 IU vitamin A palmitate/kg dry diet without supplemental β-carotene grew significantly better than fish fed 6 mg β-carotene/kg dry diet. Additionally, brook trout fed 0.6 mg β-carotene/kg dry diet (1,000 IU vitamin A activity) during the same experimental period developed pronounced eyeball protrusion at either 9° or 12.4°C.

Vitamin D

Qualitative requirements for cholecalciferol have been determined for channel catfish and rainbow trout. Lovell and Li (1978) demonstrated the essentiality of dietary cholecalciferol for channel catfish fingerlings via greater weight gain and bone mineralization (total body ash, phosphorus, and calcium) in individuals fed 500 IU cholecalciferol/kg dry diet compared with 0% dietary cholecalciferol. Hypervitaminosis was not detected since dietary cholecalciferol concentrations as high as 1,000,000 IU/kg dry diet did not suppress body weight gain nor body fixation of calcium and phosphorus. Barnett et al. (1979a) established the essentiality of cholecalciferol for rainbow trout fingerlings using two dietary concentrations (0% vitamin D_3 compared with 1,000 IU/kg dry diet). These investigators found that

symptoms of cholecalciferol deficiency included decreased weight gain and feed efficiency, marked increase in plasma triiodothyronine (T3) levels, lethargy, anorexia, increased lipid content of white muscle and liver, and clinical signs of tetany. Further study of cholecalciferol deficiency in rainbow trout indicated occurrence of tetany of the epaxial musculature (white muscle fibers) and changes in muscle ultrastructure, while red muscle fibers constituting the lateral line musculature appeared to be normal (George et al. 1979). These changes were interpreted as being indicative of disruption of calcium homeostasis. Bone ash, calcium and phosphorus, alkaline phosphatase, plasma calcium, and plasma magnesium were similar in rainbow trout fed either 1,000 IU cholecalciferol/kg dry diet or 0% cholecalciferol. Possibly, feeding dietary cholecalciferol concentrations >1,000 IU/kg to rainbow trout fingerlings would have influenced calcium, phosphorus, or magnesium content of bone or plasma. Plasma T3 concentrations of rainbow trout were unaffected by calcium supplementation of vitamin D-deficient diets and plasma and skeletal calcium levels were unaffected by a limited range of dietary vitamin D content (0 to 1,000 IU cholecalciferol/kg dry diet) (Leatherland et al. 1980).

Relative efficacy of dietary ergocalciferol compared with dietary cholecalciferol was examined in channel catfish fingerlings (Andrews et al. 1980) and rainbow trout fingerlings (Barnett et al. 1979b; Leatherland et al. 1980). Dietary concentrations of 1,000 IU/kg or less promoted similar growth rates when identical amounts of ergocalciferol and cholecalciferol were fed to channel catfish. Comparison of identical dietary concentrations of cholecalciferol and ergocalciferol above 1,000 IU/kg (2,000 to 20,000 IU/kg) resulted in greater weight gain of fingerlings fed cholecalciferol. Based upon weight gain, channel catfish fingerlings (initial mean weight = 2.3 g) require dietary cholecalciferol at greater concentrations than 1,000 IU/kg dry diet, but ≤4,000 IU/kg dry diet (Andrews et al. 1980). Slightly larger channel catfish (initial mean weight = 6.0 g) require dietary cholecalciferol at greater concentrations than 1,000 IU/kg dry diet, but ≤2,000 IU/kg dry diet. Hypervitaminosis occurred in channel catfish fed 50,000 IU/kg of ergocalciferol or cholecalciferol as evidenced by reduced weight gain and feed efficiency. However, vertebral bone ash was not affected by various dietary ergocalciferol or cholecalciferol concentrations. Leatherland et al. (1980) reported that an inverse relationship between T3, a growth stimulating hormone, and dietary vitamin D concentration (cholecalciferol or ergocalciferol) existed in rainbow trout fingerlings. They speculated that hypersecretion of T3 in fish fed vitamin D-deficient diets may be a compensatory response. Cholecalciferol concentrations of 200 or 800 IU/kg promoted slightly better growth of rainbow trout than identical concentrations of ergocalciferol (200 or 800 IU/kg). Also, 800 IU of cholecalciferol/kg was the only dietary vitamin D concentration which significantly reduced T3 concentrations of fish compared with those fed a vitamin D-deficient diet. Barnett et al. (1979b) reported that rainbow trout fingerlings require between 1,600 and 2,400 IU of cholecalciferol/kg dry diet and that cholecalciferol is three times more effective than ergocalciferol in promoting weight gain.

Vitamin E

Vitamin E has been established as an essential dietary component for chinook salmon (Woodall et al. 1964), brown trout (Poston 1965), channel catfish (Dupree 1969b; Murai and Andrews 1974), Atlantic salmon (Poston et al. 1976), common carp (Watanabe et al. 1970a; Watanabe and Takashima 1977), and rainbow trout (Cowey et al. 1981a). Vitamin E deficiency symptoms in channel catfish include poor growth, reduced food conversion, exudative diathesis, muscular dystrophy, depigmentation, fatty livers, anemia, and atrophy of pancreatic tissue (Murai and Andrews 1974). Dietary supplementation of DL-α-tocopherol (25 to 100 mg/kg) fed to channel catfish fingerlings removed all of these deficiency symptoms, whereas an antioxidant, ethoxyquin (125 mg/kg), did not significantly improve hematocrit levels or reduce incidence of muscular dystrophy. Vitamin E deficiency symptoms in chinook salmon included poor growth, exophthalmia, ascites, anemia, clubbed gills, epicarditis, and ceroid deposition in the spleen (Woodall et al. 1964). Brook trout fingerlings fed vitamin E-deficient diets had reduced growth rates, increased mortality, and lower microhematocrit values than did fish fed a diet containing 500 mg of DL-α-tocopherol acetate/kg dry diet (Poston 1965). Atlantic salmon fed vitamin E-deficient diets displayed anemia, pale gills, anisocytosis, poikilocytosis, exudative diathesis, dermal depigmentation, muscular dystrophy, and in-

creased carcass fat and water content (Poston et al. 1976).

Vitamin E has been shown to be important in reproductive physiology of fishes. Adult female common carp (initial mean weight = 100 g) fed a vitamin E-deficient diet for 17 mo displayed reduced weight gain, lower gonadosomatic index, apparent muscular dystrophy (degenerative epaxial muscles), higher muscle water content, lower muscle protein content, and lower concentrations of yolk granules and yolk vesicles in oocytes compared with individuals fed 700 mg α-tocopherol/kg dry diet (Watanabe and Takashima 1977). Also, developing ovaries of common carp fed vitamin E-deficient diets had altered polar lipid fractions in the form of lower concentrations of 20:4ω6, 20:5ω3, and 22:6ω3 and higher concentrations of 18:1ω9 and 20:3ω9.

Quantitative vitamin E requirements of fishes depend upon interaction of several factors: 1) Dietary concentration of polyunsaturated fatty acids, 2) dietary selenium concentration, 3) dietary concentrations of proxidants and antioxidants, 4) diet storage temperature, and 5) length of diet storage. Woodall et al. (1964) reported that a dietary vitamin E concentration of 5 to 30 mg α-tocopherol combined with 5% herring oil provided satisfactory growth of chinook salmon and prevented the occurrence of clinical deficiency symptoms in this species. Common carp fingerlings (initial mean weight = 1.6 g) required about 100 mg α-tocopherol/kg dry diet in order to maintain maximal growth rate and feed efficiency (Watanabe et al. 1970b). Slightly larger common carp fingerlings (initial mean weight = 6.4 g), fed 100 mg or less of DL-α-tocopheryl acetate/kg dry diet concurrently with 5% dietary methyl linoleate as the sole lipid component, displayed apparent muscular dystrophy and had less weight gain than did fish fed 300 mg DL-tocopheryl acetate/kg dry diet plus 5% methyl linoleate (Watanabe et al. 1977). Also, common carp fed 10 or 15% methyl linoleate plus 100 mg DL-α-tocopheryl acetate, had significantly less weight gain and higher occurrence of muscular dystrophy than fish fed 2 or 5% methyl linoleate plus 100 mg DL-α-tocopheryl acetate. Rainbow trout fingerlings (initial mean weight = 0.9 g) fed a diet containing 15% pollock liver oil (in the form of methyl esters) displayed general vitamin E deficiency signs (anorexia and reduced growth), after 6 wk (Watanabe et al. 1981). Diets supplemented with 50 mg α-tocopherol/kg dry diet prevented anorexia and promoted growth rates equal to those fish fed 100, 300, or 500 mg α-tocopherol/kg dry diet. However, the minimal requirement may be slightly <50 mg α-tocopherol/kg dry diet. Larger rainbow trout fingerlings (initial mean weight = 10 g) require 20 to 30 mg DL-α-tocopheryl acetate/kg dry diet when fed 1% 18:3ω3 plus 13% palmitic acid (Cowey et al. 1981a). Dietary vitamin E concentrations <20 mg DL-α-tocopheryl acetate/kg dry diet resulted in higher molar ratios of polyunsaturated fatty acid to tocopherol in rainbow trout livers. Also, in vitro ascorbic acid-stimulated peroxidation in mitochondria and microsomes was significantly higher in rainbow trout fed low dietary vitamin E concentrations (e.g., 0 and 5 mg DL-α-tocopheryl acetate/kg dry diet). Furthermore, these investigators suggested that the vitamin E requirement for rainbow trout is undoubtedly proportionally higher with increasing dietary concentrations of unsaturated fatty acids. Supplementary dietary concentrations of either 33, 66, or 99 IU of DL-α-tocopheryl acetate/kg dry diet added to 20 mg of dietary α-tocopherol/kg dry diet, produced equal growth rates, feed efficiency, and whole body percentage protein, lipid, and moisture of rainbow trout fingerlings fed 12% dietary lipid (Hung et al. 1980). In another study, diets containing 24 mg of α-tocopherol/kg dry diet combined with about 12% dietary lipid, which included 7.5% dietary, unoxidized herring oil, prevented vitamin E deficiency in rainbow trout fingerlings (Hung et al. 1981).

Vitamin K

Dietary supplementation of vitamin K for salmonids has proven beneficial in increasing hematocrit values of brook trout (Poston 1964) and lake trout (Poston 1976b), whereas vitamin K supplementation of diets fed to channel catfish did not enhance blood clotting time or hemoglobin concentrations (Murai and Andrews 1977). Growth of each of the aforementioned species was unaffected by dietary vitamin K supplementation. A dietary concentration of 1 mg menadione dimethylpyrimidinol bisulfite/kg dry diet was sufficient to provide normal coagulation and packed cell volume of lake trout blood (Poston 1976b). Murai and Andrews (1977) concluded that channel catfish have an extremely low, if any, dietary vitamin K requirement, since individuals fed a diet devoid of vitamin K had similar weight gain, blood clotting times, prothrombin times, and hematocrit values to individuals fed

up to 1.2 mg menadione sodium bisulfite/kg dry diet.

MINERALS

Calcium and Calcium-to-Phosphorus Ratios

Initial investigations indicated that calcium uptake in fish is primarily through imbibition and gill absorption rather than from dietary sources (Podoliak 1961; Simmons 1971). Nevertheless, since calcium and phosphorus are both major components of fish bone and scales, dietary calcium-to-phosphorus ratios were examined by several investigators to determine if any interactions occur between calcium and phosphorus, which might result in altered bone ash, calcium, and phosphorus content. Dietary calcium did not affect growth and feed efficiency of common carp (Ogino and Takeda 1976), channel catfish (Lovell 1977), and rainbow trout (Ogino and Takeda 1978). However, in a separate study with channel catfish, 1.5% dietary calcium induced maximal weight gain, whereas lower and higher dietary calcium concentrations produced less weight gain (Andrews et al. 1973). Optimal growth and feed conversion occurred in channel catfish fingerlings fed a 1.5:1 ratio of calcium to phosphorus (Andrews et al. 1973) and optimal feed efficiency and serum inorganic phosphorus were observed in red sea bream fed a 1:2 ratio of calcium to phosphorus (Sakamoto and Yone 1973). The difficulty in determining whether dietary calcium-to-phosphorus ratios are nutritionally significant in fish may be complicated by dietary factors such as magnesium and vitamin D or use of suboptimal calcium water concentrations in various studies. Based on the few species studied, it is unknown whether salinity determines if dietary calcium-to-phosphorus ratios are important dietary factors. Optimal dietary calcium-to-phosphorus ratios have been reported for one marine species (red sea bream) and one freshwater species (channel catfish), while no optimal ratios were reported for common carp or rainbow trout.

Phosphorus

Dietary essentiality of phosphorus has been verified for channel catfish (Andrews et al. 1973; Lovell 1978), Atlantic salmon (Ketola 1975a), red sea bream (Yone 1975), common carp (Ogino and Takeda 1976), and rainbow trout (Ogino and Takeda 1978). Deficiency symptoms in channel catfish include reduced growth, poor feed efficiency, low bone ash, and low hematocrit levels (Andrews et al. 1973), and reduced weight gain, bone ash, and bone phosphorus content (Lovell 1978). Red sea bream fed phosphorus-deficient diets contained lower vertebral ash, calcium, and phosphorus and more brittle bone structure (Yone 1975). Common carp and rainbow trout fed diets deficient in phosphorus had reduced calcium, phosphorus, and ash content of whole body and vertebrae (Ogino and Takeda 1976; Ogino and Takeda 1978, respectively). Also, Ogino and Takeda (1976) reported deformity of the frontal bone of the cranium of common carp and spondylolisthesis, brachyospondylie, and synostosis of vertebrae in phosphorus-deficient individuals.

Based on examination of limited sources of phosphorus, dietary phosphorus requirements have been reported as 0.4% or 0.42 to 0.47% for channel catfish (Gatlin et al. 1982; Lovell 1978, respectively), 0.6% inorganic phosphorus supplemented to a diet containing 0.7% phosphorus from plant sources for Atlantic salmon (Ketola 1975a), 0.68% for red sea bream (Yone 1975), 0.6 to 0.7% for common carp (Ogino and Takeda 1976), and 0.7 to 0.8% for rainbow trout (Ogino and Takeda 1978). Supplementation of 0.4 to 2% monosodium, monocalcium, or dicalcium phosphate to diets containing 0.55 to 0.65% available phosphorus did not improve growth or feed efficiency of rainbow trout fingerlings (initial mean weight = 21 g) over an 18-wk period (Reinitz et al. 1978a). Generally, inorganic phosphorus in formulated feeds is more digestible or available for fishes than organic forms of phosphorus occurring in soybean meal and fish meal (Ketola 1975a, b; Lovell 1978).

Magnesium

Magnesium is an essential constituent of bone in fish and is interrelated with calcium metabolism. Whole body and vertebral calcium content were inversely related to dietary magnesium concentration in common carp (Ogino and Chiou 1976) and rainbow trout (Ogino et al. 1978), whereas whole body and vertebral phosphorus content were unaffected by dietary magnesium in the same species. Sakamoto and Yone (1979) concluded that marine fishes have very low (if

any) dietary magnesium requirements, since 12 versus 66 mg magnesium/100 g diet fed to red sea bream did not differentially affect growth, vertebral magnesium content, or vertebral calcium content.

Quantitative dietary magnesium requirements for rainbow trout (0.06 to 0.07%) and carp (0.04 to 0.05%) were established based upon one dietary calcium concentration and one calcium and magnesium concentration in ambient water in each study (Ogino et al. 1978; Ogino and Chiou 1976, respectively). Cowey (1976) reported that excessive dietary calcium (2.7%) in relation to dietary magnesium (0.04%) was accompanied by renal nephrocalcinosis in rainbow trout, while 0.1% magnesium fed to rainbow trout along with 2.7% calcium resulted in normal renal calcium concentrations. Further increases in dietary calcium concentrations to 4% required dietary magnesium concentrations of 0.1%, rather than 0.06% magnesium to prevent renal calcinosis (Cowey et al. 1977). Therefore a direct interrelationship was established between dietary calcium and magnesium fed to rainbow trout in freshwater (Cowey 1976).

Manganese

Common carp and rainbow trout fingerlings have been found to have higher growth rates when fed 12 to 13 mg manganese/kg dry diet versus 4 mg manganese/kg dry diet (Ogino and Yang 1980). Manganese-deficient rainbow trout displayed abnormal curvature of the backbone and malformation of the tail.

Zinc

Zinc has been shown to be an essential trace element for rainbow trout in separate studies (Ogino and Yang 1978; Ketola 1979b) and common carp (Ogino and Yang 1979). Dietary zinc concentrations of 15 and 30 mg/kg dry diet fed over an 8-wk period in the presence of 11 μg zinc/l of rearing water promoted satisfactory growth of rainbow trout, while 5 mg zinc/kg dry diet produced slightly slower growth rates (Ogino and Yang 1978). In the same study, rainbow trout fingerlings fed 1 mg zinc/kg dry diet had poor growth, high mortality (46% vs. 0% in other treatments), high incidence of cataracts (49% vs. 0% in other treatments) and high incidence of fin erosion (86% vs. 0% in other treatments). Protein digestibility was appreciably reduced in rainbow trout fed 1 mg zinc/kg dry diet (Ogino and Yang 1978). Although carboxypeptidase activity was not tested, lower activity of this zinc-containing enzyme could explain lower protein digestibility (Ogino and Yang 1978). Ketola (1979b) determined that laboratory diets containing 40% white fish meal (60 mg zinc/kg dry diet) caused bilateral cataracts in rainbow trout, possibly as a result of excesses of other minerals in white fish meal (calcium, phosphorus, sodium, or potassium). Supplementation of 150 mg zinc/kg dry diet to the laboratory diet containing 40% white fish meal and 60 mg zinc/kg dry diet resulted in normal growth rates and prevented cataract formation in rainbow trout. Common carp, fed 1 ppm dietary zinc in the presence of 10 μg zinc/l rearing water over 12- and 16-wk periods in separate studies, had high mortality rates, reduced growth rate, and had fin and skin erosion (Ogino and Yang 1979). No cataract formations were reported in zinc deficient common carp, however. Common carp fingerlings required between 15 and 30 ppm of dietary zinc for optimal growth.

Iron

Dietary iron is essential for fishes to maintain normal hemoglobin content, hematocrit value, and mean corpuscular diameter. Hypochromic, microcytic anemia occurred in red sea bream (Yone 1975) and common carp (Sakamoto and Yone 1978b) as well as anisocytosis in red sea bream fed iron-deficient diets. Control diets fed to red sea bream and common carp, which prevented these iron deficiency symptoms, contained 1.2 g ferric citrate/kg dry diet and 199 mg iron/kg dry diet, respectively. A minimal dietary iron concentration of 150 mg/kg diet is required to prevent iron deficiency symptoms such as low mean corpuscular diameter and low blood iron content in red sea bream (Sakamoto and Yone 1978a).

Copper

Dietary copper requirements have been investigated for channel catfish, common carp, and rainbow trout. Copper requirements, if any, for fingerling channel catfish are $\leq$1.5 mg/kg dry diet (Murai et al. 1981). Channel catfish fed 9.5 mg copper/kg dry diet while reared in water containing 0.33 μg copper/l for 16 wk grew significantly slower than individuals fed diets containing only 3.5 mg copper/kg dry diet. Further

reductions in weight gain occurred in channel catfish fed diets containing 17.5 or 33.5 mg copper/kg dry diet compared with those individuals fed 9.5 mg copper/kg dry diet. Also, a slight reduction occurred in the number of erythrocytes and hematocrit levels in channel catfish fed 33.5 mg copper/kg dry diet resulting in slight anemia. Murai et al. (1981) suggested that since fish can absorb copper from the surrounding water, absorption of environmental copper may result in lower dietary copper requirements than that required by most terrestrial animals. Common carp fingerlings fed 0.7 mg copper/kg dry diet had lower weight gain than individuals fed 3.0 mg copper/kg dry diet (Ogino and Yang 1980). In contrast, no differential growth response occurred in rainbow trout fingerlings fed either 0.7 or 3.0 mg copper/kg dry diet (Ogino and Yang 1980).

Selenium

Selenium is an essential dietary constituent for Atlantic salmon and rainbow trout. Poston et al. (1976) demonstrated dietary essentiality of selenium for Atlantic salmon fry and fingerlings. Deficiency of dietary selenium suppressed glutathione peroxidase activity, while supplements of both vitamin E (500 IU DL-α-tocopheryl acetate/kg) and selenium (0.1 mg/kg dry diet) prevented muscular dystrophy. However, no minimal dietary selenium requirement nor minimal selenium concentration causing toxicity was determined for Atlantic salmon. Dietary selenium concentrations as low as 0.07 mg/kg dry diet prevented selenium deficiency symptoms (i.e., degeneration of liver and muscle) in rainbow trout fingerlings concurrently fed 400 IU vitamin E/kg dry diet while reared in water containing 0.4 μg selenium/l (Hilton et al. 1980). Since selenium is a component of glutathione peroxidase, it is of interest that maximal plasma glutathione peroxidase activity was obtained at a dietary selenium concentration of 0.15 to 0.38 mg/kg dry feed. On the other hand, selenium toxicity occurred in rainbow trout fed dietary selenium concentrations of 13 mg/kg of dry diet, causing reduced growth and feed efficiency and uncoordinated spiral swimming behavior 12 to 24 h before death. Hilton et al. (1980) emphasized the importance of reporting dietary vitamin E concentrations and water borne selenium concentrations when investigating dietary selenium requirements of fish.

Iodine

Iodine has been shown to have a role in thyroid metabolism in fishes similar to that occurring in terrestrial animals. Woodall and LaRoche (1964) examined dietary iodide requirements of chinook salmon fed 0.1 to 10.1 mg iodide/kg diet during an initial 6-mo study and an additional 9-mo study. After 6 mo, no significant differences occurred in growth, feed efficiency, and body composition. However, iodine stored in the thyroid glands of chinook salmon fed 0.1 mg iodide/kg dry diet equaled only 40% of the iodide in individuals fed higher iodide concentrations (0.6, 1.1, 5.1, and 10.1 mg iodide/kg dry diet). The authors concluded that the minimal dietary iodide requirement of chinook salmon fingerlings was about 0.6 mg iodide/kg dry diet based upon the iodide content in thyroid glands. Additionally, they recommended a higher dietary iodide requirement for advanced parr (1.1 mg iodide/kg dry diet) and speculated that smoltification may be accompanied by increased thyroid activity. Increased thyroid activity has been demonstrated in several salmonids during the parr-smolt transformation (Wedemeyer et al. 1980).

SUMMARY AND RECOMMENDATIONS

1) All fish species examined thus far in feeding studies require the same dietary essential amino acids (arginine, histidine, isoleucine, leucine, lysine, methionine, phenylalanine, threonine, tryptophan, and valine).
2) Optimal dietary lipid concentrations for maximal protein sparing action in most fish species range from 12 to 24%.
3) Qualitative essential fatty acid requirements and ability to elongate and desaturate fatty acids such as linoleic and linolenic acids are highly variable among fishes, indicating a need for more species-specific research.
4) Relative protein sparing action of carbohydrates and lipids is also highly variable among fish species, necessitating more species-specific research in place of approximating metabolic capabilities of an unstudied species based upon knowledge of other species.
5) Extensive research is needed to determine

nutrient requirements for the striped bass and several coolwater fish species that support important commercial or recreational fisheries, or both.

6) A better understanding of the effects of high dietary fiber on fishes is necessary to evaluate the amount of interference of fiber with enzyme action, changes in transit time of ingested feed in the digestive tract with varying dietary fiber concentrations and effects of dietary fiber on nutrient absorption of fishes.
7) Calcium and magnesium requirements in fishes should be further examined for individual species reared in different calcium and magnesium concentrations or salinities to further determine relative nutritional importance of dietary and water absorption routes of these minerals.
8) Phosphorus requirements of fishes need to be evaluated in conjunction with calcium and magnesium requirements to determine optimal dietary ratios of each macromineral.
9) Knowledge of requirements of fishes for trace elements such as selenium, copper, iron, and zinc is rare, thereby warranting additional research.
10) Better definition of quantitative nutrient requirements of brood stock of various species is necessary to ensure better quality eggs and fry.
11) Regarding better standardization of individual fish nutrition experiments, panelists from a recent fish nutrition workshop have recommended that measurements for metabolizable energy values for experimental diets and digestibility values for macronutrients should be monitored and reported. This is especially important in studies evaluating dietary protein concentration requirements and optimal protein to energy requirements of fishes. Metabolism chambers used by Smith (1971, 1976) are the preferred method.

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ANALYSIS OF DOUBLE-TAGGING EXPERIMENTS

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ABSTRACT

Statistics arising from double-tagging experiments may be applied to estimate tag-shedding probabilities directly, to estimate parameters of underlying theoretical shedding models, or to estimate mortality rates free of tag-shedding bias.

Simple maximum likelihood estimators of tag retention rates, along with their asymptotic variances, may be derived assuming conditional multinomial sampling models. If specific models of shedding are of interest, limitations of existing theory may be reduced by assuming the Type II shedding rate is time-dependent. In the more realistic models and their simpler precursors, parameters may be estimated by least squares or by maximum likelihood methods. Complications arising in the direct maximization of the conditional likelihood may be circumvented by use of iteratively reweighted Gauss-Newton algorithms available in standard statistical software packages. Simple diagnostic plots may be helpful in model selection.

When a sequence of double-tagged cohorts is released, recapture statistics may be treated separately or combined to estimate common shedding rates, but a more general linear model may be used to fully exploit the structure of the experiment and to estimate both common parameters and those unique to each cohort.

When recapture times are unknown but the experiment spans a sufficiently long period, the ratio of constant Type II tag-shedding rate to constant Type II total mortality rate may be estimated. Under similar circumstances, but with exact recapture times known for each fish, maximum likelihood estimates of both parameters may be computed.

If only the Type II mortality rate is of interest, it may be estimated free of tag-shedding bias by simple linear regression of appropriate double-tagging statistics, if Type II shedding and Type II mortality are constant during the experiment.

The estimation of fishing mortality rate, exploitation rate, and population size through mark and recapture experiments is often complicated by the incidental shedding or loss of marks. Failure to account for tag shedding may lead to biased parameter estimates. Thus a well-designed tagging experiment will incorporate some provision for estimating shedding rates and computing correction factors.

The approach usually taken is to release a group, or perhaps several groups of double-tagged fish, and then to estimate shedding rates using information on the number of fish returned in a sequence of recapture samples still bearing both tags and on the number of returns with only one tag remaining. A variety of statistical methods and estimation procedures have been developed. Papers by Beverton and Holt (1957), Gulland (1963), Chapman et al. (1965), Robson and Regier (1966), Chapman (1969), Bayliff and Mobrand (1972), Seber (1973), Laurs et al. (1976), Arnason and Mills (1981), Kirkwood (1981), and Seber and Felton (1981) are particularly noteworthy. In recent years attention has focused primarily on the regression methods developed by Chapman et al. (1965) and extended first by Bayliff and Mobrand (1972) and most recently by Kirkwood (1981).

Despite the extensive literature on double-tagging there is need for an integration of existing thought and for development of new ideas and statistical methods. Accordingly, this paper surveys basic tag-shedding theory and the most widely used analytical techniques, and describes a variety of new models and estimation procedures. Left unaddressed are several important aspects of planning double-tagging experiments. These are the subject of a companion paper by Wetherall and Yong (1981).

TAG LOSS IN SINGLE-TAGGING EXPERIMENTS

To establish a context for later derivations we begin by reviewing the process of tag loss in a population of single-tagged fish. In such a popu-

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lation, losses may be caused by fishing mortality or recapture, natural mortality, tagging mortality (mortality induced by the application or presence of the tag), permanent emigration, or by tag shedding. In addition, recaptured tags are considered "lost" if not detected in the catch and recovered, or, when recovered, if not returned or reported.

Beverton and Holt (1957) recognized two kinds of losses, which they designated Type I and Type II (these are called Type A and Type B by Ricker 1975). Type I losses are those which, in effect, reduce the number of tags initially put out. They result from the pulse of tagging mortality and tag shedding occurring immediately after release (or in a relatively brief period following release) and from the nonrecovery and nonreporting of tag recaptures. Type II losses are those happening steadily and gradually over an extended period following release of the tagged fish.

These relations may be stated more succinctly in a simple mathematical model. Let $E(r_i)$ denote the expected number of returns of tags recaptured in the ith time interval following the release of $N_s(0)$ single-tagged fish. Then

$$E(r_i) = \pi\ \rho\ N_s(0) \int_{t_i}^{t_i+\Delta_i} F(u)\ \zeta(u)\ \exp\left(-\int_0^u H(x)\ dx\right) du$$

where t_i = time at the beginning of interval i

Δ_i = length of time interval i

$1 - \pi$ = probability that a tag is lost due to immediate tagging mortality

$1 - \rho$ = probability that a tag is shed immediately following release

$F(u)$ = instantaneous fishing mortality rate at time u

$1 - \zeta(u)$ = probability that a tag recaptured at time u is not recovered and reported (a Type I loss)

$H(x)$ = total instantaneous rate of Type II tag loss at time x.

Here $H(x)$ represents the unspecified combined effects of fishing mortality, $F(x)$, natural mortality, $M(x)$, instantaneous tag shedding, $L(x)$, and remaining losses, $G(x)$. The usual assumptions are that the Type II losses operate in the manner of independent Poisson processes with constant rates and that the recovery and reporting rates also are constant. Under these conditions the model takes the familiar form

$$E(r_i) = \eta\ N_s(0)\left(\frac{F}{F+X}\right)\left(1 - \exp(-(F+X)\Delta_i)\right)\left(\exp(-(F+X)t_i)\right) \quad (1)$$

where $\eta = \pi\ \rho\ \zeta$

$X = M + L + G.$

A variety of estimation schemes based on this equation have been developed, notably by Paulik (1963). These have been reviewed along with other mark-and-recapture approaches by Cormack (1968) and Seber (1973). The importance of assumptions on Type I and Type II losses in these procedures depends on which parameters are of central concern in the experiment. In fisheries applications the parameter most often focused on is the fishing mortality rate, F. Paulik's single-release regression model with constant Δ, for estimating F and the exploitation rate, $\mu = (F/(F+M))[1 - \exp(-(F+M)\Delta)]$ stems directly from Equation (1). In this situation, if Type I losses are present the model will estimate ηF rather than F. Subsequent estimates of X will be too large. Further, estimates of the exploitation rate will be negatively biased, and if these are used along with $N_s(0)$ to estimate total population sizes, such estimates will be inflated. Of course, this is the general effect of Type I losses on Petersen estimates.

If Type II tagging mortality or Type II tag shedding occur, the estimate of F from this single-release model will not be affected, but the estimate of μ will be less than the true exploitation rate of the unmarked population.

Sometimes all recaptures are made during subintervals of equal length imbedded and irregularly spaced within the total recapture period (e.g., in a salmon fishery with a complex pattern of open and closed periods). In this case, Paulik shows that the single-release model based on Equation (1) will give estimates of F and X

which are unaffected by Type I losses, and in fact will yield an estimate of η as well as the usual estimates of F and X. Since the conditions required for this scheme will not often be encountered, it will usually be necessary to conduct a multiple-release experiment, with at least one preseason release, in order to obtain separate estimates of F, X, and η. Models appropriate to this situation have also been extensively developed by Paulik (1963).

However, even in the multiple-release models the Type II tagging mortality and Type II shedding will generate an underestimate of the true exploitation rate. Thus while the problems imposed by Type I losses may be circumvented by more elaborate experimental designs, the undesired effects of Type II losses remain. Two remedies are possible: 1) The single-tagging may be supplemented with a double-tagging experiment and other special studies to estimate Type II components and determine correction factors, or 2) double-tagging may be used exclusively to estimate mortality rates unaffected by Type I and Type II shedding. Both strategies are treated below. We note here that even when tag shedding and mortality are not the chief concerns of a tagging experiment, double-tagging is often employed simply to increase expected recovery rates (e.g., Hynd 1969; Bayliff 1973).

MODELS OF DOUBLE-TAGGING

We restrict our attention to the case where members of the population are marked with two tags differing in position of attachment and possibly type (call these Type A and Type B). We assume the burden of carrying both tags is equal to the stress of carrying either one alone. Further, we assume that the probabilities of loss are the same for each tag of a specified type and independent of the status of the other tag. Suppose a cohort of fish is double-tagged at time 0. For any fish still alive at time t, the probability that the Type A tag has been shed can be stated as

$$\Omega_A(t) = 1 - \rho_A g_A(t)$$

where $g_A(t) = \exp\left(-\int_0^t L_A(u)\, du\right)$.

An analogous expression exists with respect to tag B. Where shedding rates are assumed to be the same for tag Types A and B the subscripts can be dropped, i.e., the common probability of shedding by time t is

$$\Omega(t) = 1 - \rho g(t). \tag{2}$$

If we set $L(u) = L(\text{constant})$, Equation (2) embodies the assumptions of Bayliff and Mobrand (1972)—Type II shedding is a simple Poisson process with an identical constant rate for each tag, so that each tag has the same probability of shedding by time t. Moreover, in due course all surviving fish will have shed both tags as long as $L > 0$, i.e., $\Omega(\infty) \to 1$.

The validity of this particular set of assumptions has recently been challenged by results of tag-shedding studies with northwest Atlantic bluefin tuna, *Thunnus thynnus*, (Baglin et al. 1980) and with southern bluefin tuna, *T. maccoyii*, (Kirkwood 1981). In the former case, it was found that the Type II shedding rate increased with time. In Kirkwood's analysis it was apparent that the Type II rate decreased markedly over time. Therefore, it clearly would be advantageous to construct a model permitting time-dependent Type II shedding rates. Kirkwood approached this problem by attacking the common assumption of uniform shedding probabilities among all fish in the cohort. Instead, he considered the Type II shedding rate for each tag applied to be constant over time, but further assumed that the rate for each tag was a random variable with specified probability density. In this light, the deterministic model at Equation (2) is replaced by the expectation $J(t) = E[\Omega(t)] = 1 - \rho\, E[g(t)]$. The average time-varying shedding rate at time t may now be defined as

$$\Psi(t) = \frac{E\{g(t) \cdot L\}}{E\{g(t)\}}$$

where the expectations are taken with respect to the probability density of L. Following standard principles of reliability theory, this may be reduced to

$$\Psi(t) = -\frac{\partial \ln E\{g(t)\}}{\partial t}.$$

Under Kirkwood's assumptions $\Psi(t)$ will decrease with time as long as there is variation in shedding rate among tags, i.e., there will be a continuous culling of tags with relatively high shedding probabilities. This concept is clearly an

attractive alternative to the Bayliff-Mobrand model.

Problems in which the instantaneous loss rate is treated as a random variable arise in a variety of contexts ranging from bioassay to analysis of labor turnover in corporations. Because of its unimodality and mathematical tractability, the distribution often selected to describe this variation is the gamma distribution with mean λ and variance λ^2/b (e.g., see Bartholomew 1973:186 or McNolty et al. 1980). As Kirkwood (1981) showed, for the tag-shedding problem, this choice leads to

$$J(t) = 1 - \rho\left(\frac{b}{b + \lambda t}\right)^b \qquad (3)$$

so that

$$\Psi(t) = \frac{b\lambda}{b + \lambda t}.$$

The Bayliff-Mobrand model is now seen as a special deterministic case; when $b \to \infty$, $J(t) \to 1 - \rho \exp(-\lambda t)$ and $\Psi(t) \to \lambda$. Kirkwood considered a further elaboration of Equation (3) by assuming only a fraction of the tags, δ, will have a nonzero probability of shedding; the remainder are regarded as permanently attached. In this event the expected probability of shedding by time t is

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b\right]. \qquad (4)$$

While this approach significantly advances the realism and flexibility of tag-shedding theory, it fails to account for the apparent increase in average shedding rate as observed in the Atlantic bluefin tuna. Thus, although permitting variation in shedding rate among tags, it still considers the rate for each tag to be constant over time.

This condition is not apt to hold. As Kirkwood (1981) himself pointed out, plastic dart tags may become so firmly imbedded and overgrown by tissue as time passes that the probability of shedding approaches zero. This is most apt to occur in species which grow slowly, such as the southern bluefin tuna. On the other hand, it is well known that various metallic tags may corrode with time and their shedding probabilities increase. Plastic tags also deteriorate.

Accordingly, consider the Type II shedding rate to be a function of time, $L(t)$. A relatively simple model for this situation is $L(t) = \alpha + \beta t^{(\gamma-1)}$, permitting a wide variety of forms for the instantaneous shedding process. In general, all three parameters of this model could be specified as random variables. Thus with $\alpha > 0$, $\beta > 0$, and $-\infty < \gamma < \infty$ the probability of shedding might increase over time for some fish in a cohort, decrease for others, and be constant for the remainder. However, to simplify the analysis assume here that γ is fixed and identical for all members of the cohort. Now if α and β are independently distributed as gamma random variables we have

$$J(t) = \delta\left[1 - \rho\left(\frac{b}{b + \lambda t}\right)^b \left(\frac{\gamma c}{\gamma c + \xi t^\gamma}\right)^c\right] \qquad (5)$$

and

$$\Psi(t) = \left(\frac{b\lambda}{b + \lambda t}\right) + \left(\frac{\gamma c\ \xi t^{\gamma-1}}{\gamma c + \xi t^\gamma}\right)$$

where the new symbols are ξ, the expected value of β, and c, the reciprocal of the squared coefficient of variation of β. Hence, if between-tag variability in α and β approaches zero,

$$J(t) \to \delta\left\{1 - \rho \exp\left[-\left(\frac{\lambda t + \xi t^\gamma}{\gamma}\right)\right]\right\}$$

and $\Psi(t) \to \lambda + \xi t^{(\gamma-1)}$. In the basic model at Equation (4), for tags still in place at time t the conditional probability of shedding in the interval $(t, t + dt)$ is independent of t. In the extended model at Equation (5), this conditional probability may also increase or decrease with t depending on γ.

While elaboration of the tag-shedding equations in this manner is straightforward, it is doubtful whether a very clear discrimination between such parameter-laden models is possible given the usual recapture statistics. Distinctions between the extended models are reduced by the integration of the shedding processes over several recapture periods and are further obscured by sampling variation.

However, on the basis of these conceptual models of the tag-shedding process we can now write the well-known equations describing the expected number of tags of a specified type still attached at time t. For $N_d(0)$ fish initially double-tagged with Types A and B tags, let

$$S(t) = \pi \cdot \exp\left(-\int_0^t Z(u)du\right)$$

be the probability of survival to time t, where $1 - \pi$ = probability of immediate mortality and $Z(u) = H(u) - L(u)$ is the time dependent instantaneous death rate. Then the expected number of fish bearing a single tag of Type A at time t is $N_A(t) = N_d(0)\ S(t)\ J_B(t)(1 - J_A(t))$. An analogous expression may be written for $N_B(t)$, and if the two tags are considered identical, the subscripts A and B may be dropped to yield

$$N_s(t) = N_A(t) + N_B(t)$$

$$= 2N_d(0)\ S(t)\ J(t)\ (1 - J(t)),$$

the expected number of fish still bearing a single tag at time t.

The expected number of double-tagged fish at time t when A and B types are differentiated is $N_d(t) = N_d(0)\ S(t)(1 - J_A(t))(1 - J_B(t))$ or when no distinction is made between A and B types, $N_d(t) = N_d(0)\ S(t)(1 - J(t))^2$. In any event, the total number of fish expected at time t with one or two tags remaining is $N_\cdot(t) = N_s(t) + N_d(t)$.

The processes described above are not directly observable, so inferences about the shedding rates must be made on the basis of catch statistics. When recapture effort is exerted during a time interval we assume it is applied continuously. During a period of length Δ_i beginning at time t_i the expected number of recaptures of tagged fish in category j is therefore

$$E(r_{ji}) = \int_{t_i}^{t_i+\Delta_i} F(u)\ N_j(u)\ du \qquad (6)$$

where j = A, B, s, d, $\cdot$.

To complete the integral at Equation (6) it has been customary to make two key assumptions at this juncture (Chapman et al. 1965). First, we assume the fishing mortality rate, $F(u)$, is a step function constant within each recapture interval, i.e., $F(u) = F_i$ for $t_i < u < t_i + \Delta_i$ Second, we assume the average value of $N_j(u)$ during the interval is approximately equal to $N_j(t_i + \Delta_i/2)$. [This approximation is generally quite good for Δ_i of 1 yr or less. If $N_j(u)$ is linear over the interval the relation is exact regardless of Δ_i.] Under these conditions the set of recapture equations becomes

$$E(r_{ji}) = F_i\ \Delta_i\ N_j(\tau_i) \qquad (7)$$

where $\tau_i = t_i + \Delta_i/2$.

The standard procedures for estimating shedding rate parameters, and many of those to be described shortly, rely on a sequence of ratios of the estimated or observed number of recaptures from the various categories during successive fishing periods. It is clear from the equations above that such ratios will be functions of τ_i and the shedding parameters only, and independent of F_i, $N_d(0)$ and any parameters of the survival function $S(\tau_i)$.

Further, the ratios will be unaffected by nonrecovery or nonreturn as long as these processes operate at constant levels with respect to recaptures during a given time interval and at the same rates for each tagged fish category. Throughout this paper we assume this is so. However, this latter condition is one which could be violated easily, particularly if catches are not inspected carefully for tag recaptures. Where fish are handled individually there may be no difference in recovery rates between single- and double-tagged fish. Otherwise, recovery rates may be greater in double-tagged individuals. Once tagged fish are recovered, there may be further problems with respect to return rates. Laurs et al. (1976) in a study of shedding rates in North Pacific albacore, *T. alalunga*, and Myhre (1966) in experiments with Pacific halibut, *Hippoglossus stenolepis*, allowed for the possibility that a certain proportion of double-tagged recoveries would be misreported as having only a single tag. [For example, a fisherman might pocket one of the tags as a souvenir, or one tag might be simply lost after recapture.]

ESTIMATION OF SHEDDING RATES AND PARAMETERS

In the analysis of tag-shedding data a broad range of objectives may be pursued, and these give rise to a variety of estimation problems and approaches. Fundamentally, of course, the analyst wishes to correct systematic bias in estimates of basic population parameters caused by tag loss. There are several ways to do this. Where concurrent single-tagging and double-tagging experiments are conducted, information on shedding rates from the double-tagging may be used to compute adjustment factors, which in turn are applied to recoveries from the primary single-tagging study. Thus in single-tag estimation procedures based on Equation (1), for example, r_i would simply be replaced by

$$r_i' = r_i \kappa_i^{-1}, \tag{8}$$

where κ_i, estimated from double-tagging, is the probability that a tag will still be attached at time τ_i. If returns from the double-tagging experiment are too few to provide an estimate of κ_i for each recapture interval, interpolation is necessary. In any event, in this approach only minimal assumptions need be made about the manner in which shedding occurs.

In most treatments of tag shedding, however, a specific model is postulated for the shedding process. Once the parameters of such a model are estimated, appropriate adjustments for tag shedding are made either to the single-tag recovery data, as above, or directly to estimated population parameters. A third strategy is to conduct the experiment entirely with double-tagged fish, and to estimate mortality rates and other population parameters directly, in such a way that no corrections are necessary.

These various approaches are discussed now in greater detail, assuming a continuous recapture process. For situations in which tagged fish are recaptured once at most, but only in point samples, some estimation procedures are given by Seber (1973) and Seber and Felton (1981). For multiple-recapture models of the Jolly-Seber type, again with point sampling, the reader should consult Arnason and Mills (1981).

Estimating Adjustment Factors for Single-Tag Recoveries

Here we estimate κ_i, the probability of tag retention at time τ_i, the midpoint of the ith recapture period. We assume the shedding probabilities for each tag are identical and independent of the status of the other tag, and that recovery and reporting rates are the same for recaptured fish bearing either one tag or two. Under these conditions the number of double-tag recoveries, r_{di}, is proportional to κ_i^2 and the number recovered with only a single tag remaining, r_{si}, is proportional by the same factor to $2\kappa_i(1-\kappa_i)$. Of the total number of recoveries from the double-tagging experiment in the ith period, the proportion bearing two tags is therefore

$$P_{di} = \frac{\kappa_i}{2 - \kappa_i} .$$

Maximum likelihood (ML) estimates of the κ_i are now easily derived. We assume the conditional distribution of r_{di}, given $(r_{di} + r_{si})$, is binomial with parameter P_{di}. The likelihood of the ith recapture sample is thus

$$\mathcal{L}_i = \left(\frac{r_i!}{r_{di}!\ r_{si}!}\right)\left(\frac{\kappa_i}{2 - \kappa_i}\right)^{r_{di}}\left(1 - \frac{\kappa_i}{2 - \kappa_i}\right)^{r_{si}} .$$

The ML estimator of κ_i is easily found:

$$\hat{\kappa}_i = \frac{2r_{di}}{r_{si} + 2r_{di}} . \tag{9}$$

This result is also given by Seber (1973) under somewhat different assumptions. The asymptotic variance of $\hat{\kappa}_i$ is

$$\sigma^2_{\hat{\kappa}_i} = \frac{\kappa_i(1 - \kappa_i)\ (2 - \kappa_i)^2}{2r_{\cdot i}} . \tag{10}$$

As usual, numerical estimates are computed by inserting $\hat{\kappa}_i$ in place of κ_i.

Note that $\hat{\kappa}_i$ has a small negative statistical bias. In fact, using a Taylor series expansion it may be shown that

$$E(\hat{\kappa}_i) \simeq \kappa_i\left[1 - \frac{(1 - \kappa_i)\ (2 - \kappa_i)}{2r_{\cdot i}}\right].$$

Bias increases with time out, i.e., as κ_i decreases, and is inversely related to the total number of recaptures. When $\kappa_i = 0.5$ and $r_{\cdot i} = 10$, the negative bias in $\hat{\kappa}_i$ is $<4\%$.

Note further that since the likelihood function is conditioned on $r_{\cdot i}$, inferences based on Equations (9) and (10) apply strictly only to the particular experimental outcome being studied, and not to the broader class of results which might be obtained in replications of the experiment. Providing that the approximation in Equation (7) is valid, a more complicated unconditional model would yield the same estimate of κ_i, but the variance of $\hat{\kappa}_i$ would be greater, reflecting the stochastic nature of the mortality and recapture processes which lead to the $r_{\cdot i}$. Since our interest is in estimating shedding rates and not mortality rates, as a rule we consider only the simpler conditional likelihoods.

Above we have assumed the two tags are identical insofar as shedding rates are concerned. When they are subject to different shedding rates another set of estimators is required. Where A and B tags are identified, the number of A-

type recaptures, r_{Ai}, is proportional to $\kappa_{Ai}(1-\kappa_{Bi})$ while r_{Bi} is proportional to $\kappa_{Bi}(1-\kappa_{Ai})$. The number of double-tagged recaptures is proportional to $\kappa_{Ai}\,\kappa_{Bi}$. We assume the number of recaptures in the three classes are trinomial given $r_{Ai}+r_{Bi}+r_{di}$, with conditional probabilities

$$P_{Ai}=\frac{\kappa_{Ai}(1-\kappa_{Bi})}{1-(1-\kappa_{Ai})(1-\kappa_{Bi})}$$

$$P_{Bi}=\frac{\kappa_{Bi}(1-\kappa_{Ai})}{1-(1-\kappa_{Ai})(1-\kappa_{Bi})}$$

$$P_{di}=\frac{\kappa_{Ai}\,\kappa_{Bi}}{1-(1-\kappa_{Ai})(1-\kappa_{Bi})}\,.$$

These assumptions lead to the *ML* estimates

$$\hat{\kappa}_{Ai}=\frac{r_{di}}{r_{Bi}+r_{di}}\quad\text{and}\quad\hat{\kappa}_{Bi}=\frac{r_{di}}{r_{Ai}+r_{di}}\,.$$

Estimating Parameters of Specific Models

Regression Methods

Despite the directness and simplicity of the general adjustment procedure outlined above, most double-tag analyses have aimed at unraveling specific underlying mechanisms of the tag-shedding process. The probability of tag retention, κ_i, is then seen as a continuous function of time and a vector of model parameters, θ, to be estimated from the recapture data. In the terminology established above, $\kappa_i=1-J(\tau_i)$. Thus if $\hat{\kappa}_i$ or some transformation of $\hat{\kappa}_i$ is plotted against τ_i the form of an appropriate shedding model may be revealed. In fact, this is the approach adopted in much of the recent tag-shedding literature, and various weighted regression procedures have been developed to handle the parameter estimation. The general formulation of these is: find θ such that

$$S(\theta)=\sum_{i=1}^{n} w_i\,(y_i-f_i(\theta))^2$$

is minimum. In the two-parameter Bayliff-Mobrand model $y_i=\ln\hat{\kappa}_i$, where $\hat{\kappa}_i$ is given in Equation (9), and $f_i(\theta)=\ln\rho-L\tau_i$. In the four-parameter Kirkwood model

$$y_i=1-\hat{\kappa}_i$$

and

$$f_i(\theta)=\delta\left\{1-\rho\left(\frac{b}{b+\lambda\tau_i}\right)^b\right\}.$$

In both cases the authors suggest setting $w_i=r_i$. This is not optimal in a statistical sense, but is clearly preferable to equal weighting. It should be noted further that neither the Bayliff-Mobrand model nor the Kirkwood model is based on an explicit consideration of error structure for the observations. For example, there is considerable support in the literature for a multiplicative error in the recapture process, i.e., $r_{si}=E(r_{si})\exp(\epsilon_{si})$ and $r_{di}=E(r_{di})\exp(\epsilon_{di})$ and in this case the algebra leads one to the nonlinear model

$$\ln\left\{\frac{r_{si}}{2r_{di}}\right\}=\ln\left\{\frac{J(\tau_i)}{1-J(\tau_i)}\right\}+\epsilon_i$$

where ϵ_i has mean 0 and variance $\sigma^2_{\epsilon_i}$. Appropriate weights for this model are

$$w_i=\sigma^{-2}_{\epsilon_i}\simeq\frac{r_{si}\,r_{di}}{r_i}\,.$$

The regression models discussed here have assumed that recaptures are obtained from a single cohort of tagged fish. However, it is often the case that several lots of tagged fish are released at different times, so the recaptures in a particular interval may come from different cohorts. In this event the analysis may be applied to each of the m cohorts separately, provided these are fairly large. When multiple releases are made but the individual cohorts are small, so that relatively few recaptures are expected from each cohort, the usual procedure is to assume mortality rates and shedding rates are constant and identical for each group and to simply aggregate the recapture statistics from the several releases. Let the recapture intervals be of equal length, Δ, and let r_{sij} and r_{dij} denote the number of single-tagged and double-tagged fish from the jth cohort recaptured during the ith interval following that cohort's liberation. Employing the Bayliff-Mobrand linear regression model, one can estimate $\ln\rho$ and L in the usual manner as

$$\hat{\beta}=(X^T\,W\,X)^{-1}\,X^T\,W\,Y \qquad (11)$$

where $\beta=[\ln\rho\;\;L]^T$

$X=\{x_{ij}\}$ is the augmented data matrix

such that $x_{i1} = 1$ for all i and $x_{i2} = -(i - 1/2)\,\Delta$

$Y = \{y_i\}$ is the vector of dependent variables with elements

$$y_i = \ln\left\{\frac{2\sum_{j=1}^{m_i} r_{dij}}{\sum_{j=1}^{m_i} r_{sij} + 2\sum_{j=1}^{m_i} r_{dij}}\right\}. \qquad (12)$$

Here W is a matrix of statistical weights, and m_i is the number of cohorts for which recapture statistics are available in the ith postrelease interval. The symbol T denotes the matrix transpose.

If sufficient recaptures are obtained to analyze each cohort separately (say $r_{ij} \geq 10$) but a common shedding rate is assumed, several alternative approaches are available. First we can treat the separate releases as partial replicates of the same experiment and construct the dependent variables as the logarithms of the geometric means of individual statistics for each cohort. Thus to estimate $\ln\rho$ and L we use Equation (11) as before but now set

$$y_i = \sum_{j=1}^{m_i} \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)\Big/ m_i. \qquad (13)$$

Although as an estimator of $\ln\hat{\kappa}_i$ Equation (13) usually has slightly greater negative bias than Equation (12), such bias is negligible and the approach taken in Equation (13) has the advantage that statistical weights may be calculated empirically for cases where $m_i \geq 2$. In particular, define the ith diagonal element of W as

$$w_{ii} = m_i(m_i - 1)\left[\sum_{j=1}^{m_i}\left(\ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right) - y_i\right)^2\right]^{-1}$$

where y_i is given by Equation (13), and let $w_{ij} = 0$ for $i \neq j$. When some of the m_i are equal to 1, then the w_{ii} may be computed using the delta method as

$$w_{ii} = m_i^2\left[\sum_{j=1}^{m_i}\left(\frac{r_{sij}(r_{sij} + r_{dij})}{r_{dij}(r_{sij} + 2r_{dij})^2}\right)\right]^{-1}$$

on the assumption that the r_{dij} and r_{sij} are complementary binomial variables.

A second approach when the shedding rates are constant and the r_{ij} are sufficiently large is to treat returns from each of the m releases separately and then average the individual estimates. Thus the overall estimate of L, for example, would be

$$\hat{L} = \sum_{j=1}^{m} w_j'\,\hat{L}_j$$

where $\hat{L}_j$ is the estimated slope from the linear regression of

$$y_{ij} = \ln\left(\frac{2r_{dij}}{r_{sij} + 2r_{dij}}\right)$$

on τ_i. Here the individual estimate of L from the jth cohort is given a weight w_j' inversely proportional to its relative variance. In practice we substitute the statistic

$$\hat{w}_j' = \frac{\hat{\sigma}^{-2}_{\hat{L}_j}}{\sum_{j=1}^{m} \hat{\sigma}^{-2}_{\hat{L}_j}},$$

$\hat{\sigma}^{-2}_{\hat{L}_j}$ being the estimated variance of L_j computed in the jth regression. For the regression analysis itself, appropriate statistical weights for the y_{ij} would be proportional to

$$\hat{\sigma}^{-2}_{y_{ij}} = \frac{r_{dij}\,(r_{sij} + 2r_{dij})^2}{r_{sij}\,(r_{sij} + r_{dij})}.$$

Finally, the variance of $\hat{L}$ may be estimated as

$$\hat{\sigma}^2_{\hat{L}} = \sum_{j=1}^{m} \hat{w}_j'^2\,\hat{\sigma}^2_{\hat{L}_j} = \left[\sum_{j=1}^{m} \hat{\sigma}^{-2}_{\hat{L}_j}\right]^{-1}.$$

A third approach is to assume that the set of regression estimates from the m cohorts are sampled from an underlying but unspecified stochastic process which, with respect to the estimation of Type II shedding rate, has mean L and variance $\sigma^2_{\hat{L}}$. The regressions of y_{ij} on τ_i are unweighted, and empirical estimates of L and $\sigma^2_{\hat{L}}$ are given very simply by

$$\hat{L} = \sum_{j=1}^{m} \hat{L}_j\Big/ m$$

and

$$\hat{\sigma}^2_{\hat{L}} = \sum_{j=1}^{m} (\hat{L}_j - \hat{L})^2\Big/ m(m - 1),$$

where $\hat{L}_j$ is the regression estimate corresponding to the jth cohort.

A shortcoming of many double-tag analyses is that attention has been focused on estimating constant ρ and L despite the existence of multiple-release statistics. In fact the multiple-release experiment permits a more elaborate assessment of shedding processes, with the level of detail determined by specific characteristics of the experimental design. To illustrate this, consider an experiment with six recapture periods of equal length, Δ. Two cohorts of double-tagged fish are released, at the beginning of the first and fourth periods. We assume there is a unique Type I shedding rate associated with each cohort, and that the Type II shedding rate is the same for each group but is a function of time following release. Specifically, we assume the latter rate is constant for two recapture intervals following the release of any cohort, may then change to another constant level for two more periods, and so on.

The recapture statistics from the experiment may be arrayed as follows:

	Recapture interval:					
Release group	*1*	*2*	*3*	*4*	*5*	*6*
1	r_{s11}	r_{s12}	r_{s13}	r_{s14}	r_{s15}	r_{s16}
	r_{d11}	r_{d12}	r_{d13}	r_{d14}	r_{d15}	r_{d16}
2				r_{s21}	r_{s22}	r_{s23}
				r_{d21}	r_{d22}	r_{d23}

Note that $m_1 = m_2 = m_3 = 2$ and $m_4 = m_5 = m_6 = 1$.

The parameter vector $\beta = [\ln\rho_1 \ln\rho_2 L_1 L_2 L_3]^T$ may now be estimated from Equation (11) with Y as given in Equation (13) and the data matrix defined as

$$X = \begin{bmatrix} 1/2 & 1/2 & -\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -3\Delta/2 & 0 & 0 \\ 1/2 & 1/2 & -2\Delta & -\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -3\Delta/2 & 0 \\ 1 & 0 & -2\Delta & -2\Delta & -\Delta/2 \\ 1 & 0 & -2\Delta & -2\Delta & -3\Delta/2 \end{bmatrix}.$$

As usual, the covariance matrix of $\hat{\beta}$ is estimated by $\hat{V} = (X^T W X)^{-1}$.

With a little imagination this general linear model can easily be adapted to accommodate a wide variety of multiple-release experimental designs. Standard analysis of covariance techniques may be applied to test the associated hypotheses concerning β.

Maximum Likelihood Methods

As an alternative to the least squares methods we now describe some *ML* procedures for estimating the model parameters in the single-release case. Given the total number of recaptures in the ith period we again assume the numbers falling in the various classes are multinomially distributed. Thus when the A and B tags are identical there are just two classes, and the numbers in each are binomial variables with conditional expectations

$$\begin{aligned} E(r_{di}) &= r_{\cdot i} \quad P_{di} \\ &= r_{\cdot i}\left\{\frac{1 - J(\tau_i)}{1 + J(\tau_i)}\right\} \\ &= r_{\cdot i}\left\{\frac{[1 - J(\tau_i)]^2}{1 - J(\tau_i)^2}\right\} \end{aligned}$$

and $E(r_{si}) = r_{\cdot i}(1 - P_{di})$. Assuming further that the statistics for successive periods are mutually independent, the joint likelihood function for the double-tag recovery data $\{r_{d1}, r_{d2}, \ldots, r_{dn}\}$ given $\{r_{\cdot 1}, r_{\cdot 2}, \ldots, r_{\cdot n}\}$ is

$$\mathfrak{L} = \prod_{i=1}^{n}\left(\frac{r_{\cdot i}!}{r_{di}!\ r_{si}!}\right) P_{di}^{\,r_{di}}(1 - P_{di})^{r_{si}} \qquad (14)$$

where P_{di} is a function of τ_i and the vector of parameters to be estimated, θ.

When the A and B tags are not identical, the recaptures are partitioned into three disjoint classes, and the numbers in each are trinomial with expectations

$$E(r_{Ai}) = \frac{J_B(\tau_i)\,(1 - J_A(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} = r_{\cdot i}\, P_{Ai}$$

$$E(r_{Bi}) = \frac{J_A(\tau_i)\,(1 - J_B(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} = r_{\cdot i}\, P_{Bi}$$

and

$$\begin{aligned} E(r_{di}) &= \frac{(1 - J_A(\tau_i))\,(1 - J_B(\tau_i))}{1 - J_B(\tau_i)\,J_A(\tau_i)}\, r_{\cdot i} \\ &= r_{\cdot i}\,(1 - P_{Ai} - P_{Bi}). \end{aligned}$$

Now the joint conditional likelihood of the recapture sample is

$$\mathfrak{L} = \prod_{i=1}^{n} \left(\frac{r_i!}{r_{Ai}!\ r_{Bi}!\ r_{di}!} \right) P_{Ai}^{\ r_{Ai}}\ P_{Bi}^{\ r_{Bi}} \times (1 - P_{Ai} - P_{Bi})^{r_{di}}.$$

In either case, once the underlying model and the corresponding elements of θ are identified, the *ML* estimates of θ may be computed by maximizing $\mathfrak{L}$ directly using a variety of iterative search procedures. In some situations the derivatives of $\mathfrak{L}$ with respect to θ are easily derived, but even then only numerical solutions are possible.

For example, when A and B tags are identical and $J(\tau_i) = 1 - \rho(\exp(-L\tau_i))$, the *ML* estimates of ρ and L are found by solving the system of equations

$$0 = \sum_{i=1}^{n} \tau_i\ C_i \quad \text{and} \quad 0 = \sum_{i=1}^{n} C_i$$

where $C_i = \dfrac{(1 + P_{di})\ (r_{di} - P_{di}\ r_i)}{1 - P_{di}}$

$$= J(\tau_i)^{-1} \left\{ r_{di} - r_i \left(\frac{1 - J(\tau_i)}{1 + J(\tau_i)} \right) \right\}$$

$$= J(\tau_i)^{-1} \{ r_{di} - E(r_{di}) \}.$$

The asymptotic covariance matrix of $\hat{L}$ and $\hat{\rho}$ may then be derived in the usual manner by inverting the corresponding negative information matrix

$$I = \begin{bmatrix} \sum_{i=1}^{n} \tau_i^2\ D_i & -\frac{1}{\rho} \sum_{i=1}^{n} \tau_i\ D_i \\ -\frac{1}{\rho} \sum_{i=1}^{n} \tau_i\ D_i & \frac{1}{\rho^2} \sum_{i=1}^{n} D_i \end{bmatrix}$$

where $D_i = \dfrac{r_i\ P_{di}\ (1 + P_{di})^2}{1 - P_{di}}$.

Explicit analytical solutions are possible when there is only a single recapture period centered at τ and the model is reduced to a one-parameter function of either the Type I or Type II shedding rate, i.e., either $J(\tau) = 1 - \exp(-L\tau)$ or $J(\tau) = 1 - \rho$. In this event the *ML* estimate of L (with $\rho = 1$) is

$$\hat{L} = -\frac{1}{\tau} \ln \left\{ \frac{2r_d}{r_s + 2r_d} \right\} \tag{15}$$

with asymptotic variance estimated by

$$\hat{\sigma}^2_{\hat{L}} = \frac{r_s\ (r_s + r_d)}{\tau^2 r_d\ (r_s + 2r_d)^2},$$

or when shedding is a function of ρ only (with $L = 0$)

$$\hat{\rho} = \frac{2r_d}{r_s + 2r_d} \tag{16}$$

and

$$\hat{\sigma}^2_{\hat{\rho}} = \frac{r_s\ 2r_d}{(r_s + 2r_d)^3}.$$

In the case of identical A and B tags a convenient alternative to direct maximization of the likelihood function is to fit the recapture data to their expectations using an iteratively reweighted Gauss-Newton algorithm. To accomplish this one may use routines available in certain standard statistical software packages, e.g., BMDP[2]. Specifically, we find an admissible value of θ which minimizes the sum of squares

$$S' = \sum_{i=1}^{n} w_i [r_{di} - E(r_{di})]^2.$$

Since the r_{di} are assumed to be binomial (i.e., of "regular exponential" form), minimizing S' with a Gauss-Newton routine is equivalent to maximizing the likelihood of Equation (14) provided the weights used are the reciprocals of the variances of the r_{di} and are recomputed at each iteration based on the current parameter values (Wedderburn 1974; Jennrich and Moore 1975; Jennrich and Ralston 1978). In this case the weights must be $\tilde{w}_i = [r_i \tilde{P}_{di} (1 - \tilde{P}_{di})]^{-1}$, where $\tilde{P}_{di}$ is the function P_{di} evaluated at the current parameter estimates. Asymptotic standard errors for the parameter estimates are also computed by the BMDP routine.

A similar device may be used when a distinction is made between A and B tags. Given $r_{Ai} + r_{di}$ we assume r_{di} is binomial with expectation $E_B(r_{di}) = (r_{Ai} + r_{di})\ (1 - J_B(\tau_i))$. Analogously,

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

$E_A(r_{di}) = (r_{Bi} + r_{di})(1 - J_A(\tau_i))$. Thus an iteratively reweighted Gauss-Newton algorithm minimizing

$$S'_B = \sum_{i=1}^{n} w_{Bi}(r_{di} - E_B(r_{di}))^2$$

with $w_{Bi} = \tilde{w}_{Bi} = [(r_{Ai} + r_{di})\tilde{J}_B(\tau_i)(1 - \tilde{J}_B(\tau_i))]^{-1}$ is used to compute ML estimates of shedding parameters for the B class of tags. A parallel procedure gives ML estimates of parameters for the A class. Note that the two sets of parameter estimates are not independent.

Unknown Recapture Times

A tacit assumption in the foregoing procedures is that the time between release and recapture for each returned fish is known to "interval accuracy," and that exact recapture time information is available for only a fraction of the recoveries, so that all recoveries are grouped into the n time intervals to permit estimation. This will often be the case. However, in some fisheries it is conceivable that only the crudest sort of information is available on recapture times. For estimation purposes, all that is known is r_d and r_s, the total number of recaptures in each class over the experimental period $(0, T)$. When T is relatively small, say 1 yr or less, then estimation of a single Type I or Type II shedding parameter is possible, as in Equation (15) or (16). In an experiment of longer duration this is not feasible. However, it is possible under certain circumstances to estimate the ratio of the Type II shedding rate to other Type II losses. Let fishing be constant, continuous, and uniform at an instantaneous rate F. Assume further that the total instantaneous mortality rate is a constant, Z, and that shedding of tags occurs at an instantaneous rate L. If there are no Type I losses, the ratio of $E(r_s)$ to $E(r_d)$ in a double-tagging experiment approaches

$$x = \frac{2L}{Z + L}$$

as $T \to \infty$. Thus if $L = aZ$, a moment estimator of a is provided by

$$\hat{a} = \frac{\hat{x}}{2 - \hat{x}} = \frac{r_s}{2r_d - r_s}, \quad 0 \le \frac{r_s}{r_d} < 2 \qquad (17)$$

and if one has an estimate of Z which has a systematic bias due to Type II shedding, say Z^*, then a corrected estimate may be obtained, i.e., $Z^* = Z^*(1 + \hat{a})^{-1}$.

This method may also be used where single-tagging and double-tagging experiments are run concurrently. Then if $N_d(0)$ fish are released double-tagged and $N_s(0)$ with single tags, let r'_d and r'_s be recaptures from each group still bearing the initial complement of tags. Under the same assumptions as above this leads to

$$\hat{a} = \frac{r'_s N_d(0) - r'_d N_s(0)}{2r'_d N_s(0) - r'_s N_d(0)}, \quad 1 \le \frac{r'_s N_d(0)}{r'_d N_s(0)} < 2.$$

Exact Recapture Times

Turning now to the other end of the spectrum, under ideal conditions it is possible that the exact time out will be known for each fish returned. When exact recapture times are available for all fish the returns from a single-tagging experiment may be analyzed using ML procedures first developed by Gulland (1955) and later elaborated by Chapman (1961) and Paulik (1963). These rest on the assumption of binomial recapture probabilities based on constant Type II loss rates and on a resulting conditional recapture time distribution which is truncated negative exponential. Chapman et al. (1965) extended the same concepts to returns of fish initially double-tagged and still retaining both tags upon recapture, and showed that the difference between the estimated total Type II loss rate in a double-tagging experiment and the corresponding total Type II loss rate in a single-tagging study yielded an estimate of L. They noted that this is the best estimate of L possible using only the recapture information from a single-tagging experiment and from fish put out and returned with two tags. Left open was the possibility of combining this information with recapture times for fish initially double-tagged but returned with only one tag still attached. For this class of fish the distribution of recapture times is more complicated.

We now consider an exact recapture time model for an experiment based exclusively on fish initially double-tagged. Suppose $N_d(0)$ double-tagged fish are released at time 0. Over the course of the experiment, terminating at time T, a total of r_d fish are recaptured and returned with both tags intact, and r_s with only a single tag remaining. In addition, for each tagged fish returned

we assume the exact recapture time is known, i.e., we know $\{t_{s1}, t_{s2}, ..., t_{sr_s}\}$ and $\{t_{d1}, t_{d2}, ..., t_{dr_d}\}$.

Let $\Phi_d = Pr$ {fish is returned with both tags intact in $(0, T)$} and $\Phi_s = Pr$ {fish is returned with one tag remaining in $(0, T)$}. Then, assuming independence between fish and between the two tags initially applied, the numbers of returns in the various classes are trinomial random variables, i.e.,

$$Pr\{r_d, r_s\} = \frac{N_d(0)!}{r_d!\, r_s!\, (N_d(0) - r_d - r_s)!} \times \Phi_s^{r_s}\, \Phi_d^{r_d}(1 - \Phi_s\, \Phi_d)^{N_d(0)-r_s-r_d}.$$

Following principles set out previously we write the recapture probabilities as

$$\Phi_s = 2\int_0^T F(u)\, S(u)\, J(u)\, (1 - J(u))\, du$$

and

$$\Phi_d = \int_0^T F(u)\, S(u)\, (1 - J(u))^2\, du.$$

Further, the conditional probability densities for recapture times are

$$f_s(t) = \begin{cases} 2F(t)\, S(t)\, J(t)(1 - J(t))/\Phi_s & 0 < t < T \\ 0 & \text{otherwise} \end{cases}$$

$$f_d(t) = \begin{cases} F(t)\, S(t)(1 - J(t))^2/\Phi_d & 0 < t < T \\ 0 & \text{otherwise.} \end{cases}$$

The joint likelihood function for the observed numbers of single- and double-tag recoveries and the respective sets of recapture times may now be written as

$$\mathfrak{L} = Pr\{r_d, r_s\} \prod_{i=1}^{r_s} f_s(t_{si}) \prod_{i=1}^{r_d} f_d(t_{di}).$$

For specified forms of $F(u)$, $S(u)$, and $J(u)$ computation of ML estimates may now be contemplated, although the form of $\mathfrak{L}$ is apt to be exceedingly complex in most situations. For example, taking the most elementary case, assume that $J(u) = 1 - \exp(-Lu)$, $S(u) = \exp[-(M + F)u]$ and $F(u) = F$ for $0 < u < T$. Also let $T \to \infty$. Under these conditions the log-likelihood becomes

$$\ln \mathfrak{L} = \mathrm{K} + r_\cdot \ln F + (N_d(0) - r_\cdot) \times \ln\left(1 - \frac{2LF^2}{(F + M + L)(F + M + 2L)^2}\right) - (F + M)\, T_\cdot - L(T_s + 2T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si}))$$

where K is a function of the observations only,

$$T_s = \sum_{i=1}^{r_s} t_{si}, \qquad T_d = \sum_{i=1}^{r_d} t_{di},$$

$$T_\cdot = T_s + T_d, \quad \text{and} \quad r_\cdot = r_s + r_d.$$

Using numerical methods this may now be maximized as a function of F, M, and L in the usual manner to yield ML estimates of these parameters, as well as asymptotic variance estimates.

A simpler approach which yields information on $Z = F + M$ and L is to condition the likelihood of r_d and r_s on the total number of recaptures, $r_\cdot$, i.e.,

$$Pr\{r_d, r_s\} = \left(\frac{r_\cdot!}{r_s!\, r_d!}\right)\left(\frac{\Phi_s}{\Phi_s + \Phi_d}\right)^{r_s}\left(\frac{\Phi_d}{\Phi_s + \Phi_d}\right)^{r_d}.$$

This gives the log-likelihood

$$\ln \mathfrak{L} = \mathrm{K}' + r_\cdot\{\ln(Z + L) + \ln(Z + 2L) - \ln(Z + 3L)\} - ZT_\cdot - L(T_\cdot + T_d) + \sum_{i=1}^{r_s} \ln(1 - \exp(-Lt_{si})) \qquad (18)$$

where K' is independent of Z and L.

Differentiating Equation (18) with respect to Z and L and setting the derivatives to zero one finds that the ML estimates of Z and L satisfy, among other relations, the equation

$$\frac{T_\cdot}{r_\cdot} = \frac{1}{Z + L} + \frac{1}{Z + 2L} - \frac{1}{Z + 3L}.$$

Combining this with the result at Equation (17) leads immediately to a solution for $\hat{Z}$, i.e.,

$$\hat{Z} = \frac{r_{\cdot}}{T_{\cdot}}\left[\frac{1}{1+\hat{a}} + \frac{1}{1+2\hat{a}} - \frac{1}{1+3\hat{a}}\right]$$

whence $\hat{L} = \hat{a}\ \hat{Z}$.

Estimating Mortality Rates by Double-Tagging All Fish

In most of the preceding sections we assumed the basic purpose in double-tagging was to provide auxilliary information on shedding rates which could then be applied to correct recapture statistics or mortality rate estimates obtained in a primary single-tagging experiment. An attractive alternative is to use double-tagged fish entirely and to estimate the mortality rates and other vital parameters in such a way that no bias corrections are necessary. If exact recapture times are recorded, the *ML* model just discussed is appropriate. When recapture data are grouped into n time intervals of length Δ_i centered at times τ_i, a convenient context for developing this approach is the single-tagging regression model suggested by Chapman (1961) and discussed further by Cormack (1968) and Seber (1973). This takes the form

$$\ln\left(\frac{r_i}{f_i\ \Delta_i}\right) = \ln[q\rho N_s(0)] - q f_i' - X\tau_i + e_i \quad (19)$$

where f_i = the nominal fishing effort during period i

$f_i' = \sum_{j=1}^{i-1} f_j \Delta_j + \frac{f_i \Delta_i}{2}$ = the estimated nominal effort up to time τ_i

q = the catchability coefficient

e_i = a random error term.

In this particular model one obtains estimates of q and X, and, since $N_s(0)$ is known, an estimate of ρ as well. However, in the presence of Type II shedding the exploitation rate for any period will be underestimated, i.e., hidden in $\hat{X}$ will be the term L. The usual procedure would be to correct $\hat{X}$ by subtracting $\hat{L}$, where $\hat{L}$ is obtained in an independent double-tagging experiment. Instead, if we apply the model directly to recapture statistics from a double-tagging experiment ($N_d(0)$ fish initially double-tagged) we will obtain an estimate of X unaffected by Type II losses and in need of no corrections. This is accomplished by substituting the dependent variable

$$\ln\left\{\left(\frac{r_{si} + 2r_{di}}{2\Delta_i\ f_i}\right)\Big/\left(\frac{2r_{di}}{r_{si} + 2r_{di}}\right)\right\}. \quad (20)$$

Further, it now transpires that the estimate of the regression intercept term is free of Type I shedding effects, i.e., one will estimate $\ln[qN_d(0)]$ rather than $\ln[q\rho N_d(0)]$.

If we assume r_{si} and r_{di} are complementary binomial variables given r_i, and that r_i is Poisson, then approximately correct weights for the regression employing Equation (20) are

$$w_i = \left[\frac{1}{r_i}\left(1 + \frac{r_{si}^3}{(r_{si} + 2r_{di})^2\ r_{di}}\right)\right]^{-1}.$$

When effort statistics are not available so that a constant fishing mortality rate must be assumed, or when there is a linear dependence between the two independent variables f_i' and τ_i, then separate estimates of q and X are not possible using the single-tag model of Equation (19) unless Type I errors are absent. Nor is ρ estimable. Instead, one may only regress $\ln(r_i/\Delta_i)$ on τ_i to yield estimates of $\ln[\rho F N_s(0)]$ and $(F+X)$. But when the model is applied to a double-tagging experiment under the same restrictions, it is still possible to estimate both q and X unaffected by shedding.

Note that the dependent variable of Equation (20) from the double-tagging experiment is analogous to the one of Equation (19) appropriately corrected for tag shedding, as in Equation (8). In both cases the recaptures r_{di} and r_{si} are assumed to be point samples taken exactly at τ_i. Thus while in the example above $\kappa_i = \rho \exp(-L\tau_i)$, the correction procedure of Equation (8) and the method outlined here are independent of assumptions on the manner of tag shedding (cf. Seber 1973:281), provided the recapture intervals are reasonably small (say 1 yr or less).

SUMMARY AND CONCLUSIONS

The aim of this paper has been to extend the theory and methodology of estimating tag-shedding rates through double-tagging. Attention was focused on the situation most commonly encountered in fishery applications, wherein two identical tags are placed on each member of an

experimental cohort, tagged fish are recaptured at most once in a fishery which is essentially continuous, and the time at liberty is known exactly for only a fraction of the recapture sample.

The regression models studied by Chapman et al. (1965), Bayliff and Mobrand (1972), and Kirkwood (1981) were extended to permit the Type II shedding rate for each tagged fish to be a function of time. Both deterministic and stochastic versions were presented and previously published models were shown to be special cases.

If all tags are subject to the risk of shedding, i.e., if $\delta = 1$, and if data are available from several recapture periods, a simple plot of $\ln\hat{\kappa}_i$ against τ_i will reveal whether the average Type II shedding rate, $\Psi(t)$, is constant; if it is, the relationship will be linear. In this event the most parsimonious model consistent with the data will be the deterministic model based on a constant Type II shedding rate, L. In addition, if the points suggest a negative intercept on the ordinate the Type I retention rate, ρ, may be added to the parameter set. One may then carry out the parameter estimation using either the Bayliff-Mobrand linear regression model, or the nonlinear regression of $\ln(r_{si}/2r_{di})$ on τ_i, depending on which error structure is assumed. However, since the plot of $\ln\hat{\kappa}_i$ versus τ_i is approximately linear even with multiplicative error in the recapture process, it probably makes little difference which estimation method is used as long as proper statistical weights are incorporated.

If $\delta = 1$ and the plot of $\ln\hat{\kappa}_i$ versus τ_i is nonlinear, one of the more complicated tag-shedding models is called for. A trend which is concave downward suggests that $\Psi(t)$ is increasing with time and points to the stochastic model of Equation (5) or its deterministic counterpart. On the other hand, upward concavity could be explained either by a model in which the Type II shedding rate decreased with time or by Kirkwood's (1981) hypothesis, or by a combination of the two as in Equation (5).

Another useful diagnostic plot is $1 - \kappa_i$ against τ_i. These are the variables considered in Kirkwood's nonlinear model. When L is constant the plotted points will be traced by a line analogous to a von Bertalanffy growth curve with asymptote δ and location parameter ρ, and they should indicate which of these two parameters to include in the model and how much precision to expect in the resulting estimates. (In passing, it is worth mentioning that if δ is to be estimated jointly with L, a longer experiment is required to ensure high precision in the parameter estimates than if L alone is being estimated.)

The treatment of recaptures from double-tagging experiments with multiple cohorts was discussed in the context of the Bayliff-Mobrand model. Alternative methods of combining information from several cohorts to estimate common shedding parameters were proposed, and a general linear model approach was suggested for situations where more elaborate structural assumptions are made. A full numerical evaluation of these procedures remains to be done.

As an alternative to the least squares regression methods usually employed, some new *ML* procedures were presented. These are more difficult to use than the regression techniques, but offer advantages in some situations. For example, when only two recapture periods are possible one cannot compute the precision of regression estimates in the Bayliff-Mobrand model, but standard errors in the equivalent *ML* model are still estimable. The most promising method for deriving *ML* estimates in the general case may be the iteratively reweighted Gauss-Newton algorithm. Indeed, if one has access to the right computer software (such as the BMDPAR and BMDP3R programs supplied by BMDP) this approach is nearly as easy to use as the simple Bayliff-Mobrand linear regression method. A sensible procedure would be to first study the diagnostic plots suggested above for the regression analysis, and then fit the selected model using an iteratively reweighted least squares algorithm.

The estimation procedures discussed above are applicable when data are grouped by recapture interval. For situations in which the exact time at liberty is known for each recapture an unconditional *ML* model was developed. This may be applied not only to estimate shedding rates but also to estimate mortality rates unaffected by shedding. However, in its general form the likelihood function is rather complicated and only numerical solutions would be possible in most situations. Analytical estimators for L and Z were derived for a simplified conditional likelihood. Besides the more stringent data requirements this model requires the extra assumption of constant mortality rates during the experiment.

In the final section it was shown that through double-tagging it is possible to estimate mortality rates free of tag-shedding biases even when the recapture data are available only to interval-

accuracy, and without resort to the usual concurrent single-tagging experiment. The model was developed in the simple context of a fixed Type II shedding rate, but the principle applies to more complicated shedding processes as well. If the burden imposed by the second tag can be neglected, it therefore seems advantageous to double-tag all fish. In any case, when shedding is appreciable the greater overall recovery rates from double-tagging make the exclusive use of double-tagged fish a proposition well worth considering.

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FOUR NEW SPECIES OF SQUID (OEGOPSIDA: *ENOPLOTEUTHIS*) FROM THE CENTRAL PACIFIC AND A DESCRIPTION OF ADULT *ENOPLOTEUTHIS RETICULATA*

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ABSTRACT

Four new species of *Enoploteuthis* (*E. obliqua*, *E. octolineata*, *E. jonesi*, and *E. higginsi*) are described, illustrated, and compared. Adults of *E. reticulata* Rancurel 1970 are described for the first time. A key for all the species is provided.

Cephalopods are important fisheries resources in the Pacific Ocean. Thus, clarification of cephalopod systematics, particularly from areas where they are not thoroughly known such as the central Pacific, is important. Because enoploteuthid squids are deepwater animals that are not easily accessible or profitable to fish, they are not at present generally exploited commercially. In Toyama Bay, Sea of Japan, however, the enoploteuthid squid *Watasenia scintillans* (Berry 1911) is fished regularly in the spring and early summer when swarms of this species migrate to the surface to spawn (Sasaki 1914).

Cephalopods also play important roles in marine food webs. They are the principal food of many marine mammals, fishes, and some birds. Reintjes and King (1953) found that 26% of the aggregate total volume of the stomach contents of yellowfin tuna, *Thunnus albacares*, captured in the central Pacific consisted of cephalopods. King and Ikehara (1956) showed that as much as 33% of the food of the bigeye tuna, *T. obesus*, were squids, including *Enoploteuthis* sp.

Berry (1914) reported on the cephalopods collected on board the U.S. Fish Commission steamer *Albatross* from the Hawaiian area; the collection included enoploteuthid squids but none of them of the genus *Enoploteuthis*. Species of *Enoploteuthis* from Hawaiian waters and the central Pacific are described here for the first time and compared with all the known species of *Enoploteuthis* in the world.

Four new species of pelagic squids belonging to the genus *Enoploteuthis*, together with some adults of *E. reticulata*, were identified during the examination of the large collection of cephalopods at the Honolulu Laboratory, Southwest Fisheries Center of the National Marine Fisheries Service (NMFS), Honolulu, Hawaii (formerly Bureau of Commercial Fisheries Biological Laboratory, Honolulu).

The squids were taken from various areas of the central Pacific on several research vessels operated by the Honolulu Laboratory from 1953 to 1970. The fishing gear was either a modified Cobb trawl, a 10-ft Isaacs-Kidd trawl, or a Nanaimo trawl. The depth of fishing generally was between 50 and 100 m; most of the fishing was done at night.

Details on the capture of the cephalopods reported on here, including all holotypes and paratypes, are available from the original cruise reports and logs on file at the Honolulu Laboratory.

Type specimens are deposited in the cephalopod collections of the Division of Mollusks, U.S. National Museum of Natural History (USNM), Smithsonian Institution.

The terminology of the anatomical parts, measurements, and indices conform to those generally used for squids and in particular to those listed and defined by Roper (1966): ML = mantle length, CH = club hooks, CS = club suckers, MWI = mantle width index, HWI = head width index, FLI = fin length index, FWI = fin width index, ALI = arm length index, and TLI = tentacle length index. As in Roper (1966) the arm length is measured from the first basal hook (or sucker) to the tip of the arm.

The ranges and means of indices given in the descriptions were computed from measurements of the male and female specimens listed in Tables 1 to 5. This is not applicable to indices in-

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cluded in the remarks on immature individuals; not all their measurements are presented in the tables.

The following abbreviations which appear in the list of material refer to the research vessels: HMS = *Hugh M. Smith*, CHG = *Charles H. Gilbert*, and TC = *Townsend Cromwell*. A + sign after numbers in the text and tables indicates a missing mantle or arm tip, or lost suckers.

FAMILY ENOPLOTEUTHIDAE PFEFFER 1900

Genus *Enoploteuthis* Orbigny 1848

Diagnosis: Enoploteuthids with numerous light organs on mantle, head, and arms; single row of small light organs on ventral surface of eyeball; two rows of hooks on tentacular club; buccal connectives DDVD[2]; fins lateral; and mantle projecting posteriorly as free "tail."

Type species: *Loligo leptura* Leach 1817; Hoyle 1910:409, by elimination.

Enoploteuthis obliqua n. sp.
(Figs. 1, 2A; Table 1)

Enoploteuthis sp. (No. 2), Okutani 1974: figures 12c, d, f.

Holotype: Male, ML 55 mm, TC-48, Stn. 11, 11°47′N, 144°47′W, 31 March-1 April 1970, 50 m, USNM 729722.

Paratypes: 1 female, ML 50 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 577605. 1 male, ML 41 mm, TC-46, Stn. 9, 11°49′N, 144°51′W, 14 October 1969, 50 m, USNM 729713. 1 male, ML 58 mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m, USNM 729688.

Other material: 5 specimens, ML 12-17 mm, TC-43, Stn. 10, 12°03′N, 144°55′W, 8 May 1969, 50 m. 16 specimens, ML 5-18 mm, TC-43, Stn. 14, 11°56′N, 144°56′W, 10 May 1969, 50 m. 5 specimens, ML 12-17 mm, TC-43, Stn. 22, 07°41′N, 145°01′W, 13 May 1969, 50 m. 1 female (from *Alepisaurus* stomach contents), ML 50 mm, TC-44, equatorial central Pacific, July-August 1969, 10-100 m, USNM 729716. 2 specimens, ML 5 and 10 mm, TC-44, Stn. 16, 11°51′N, 144°41′W, 11 July 1969, surface. 1 specimen (from *Alepisaurus* stomach contents), ML 27 mm, TC-44, Stn. 17, 11°N, 144°W, 10 July 1969. 2 specimens, ML 12 and 17 mm, TC-44, Stn. 18, 11°53.2′N, 144°49.3′W, 11 July 1969, 100 m. 1 male, ML 37+ mm, 4 specimens, ML 12-20 mm, TC-44, Stn. 24, 07°32.9′N, 145°58′W, 13 July 1969, 50 m. 1 specimen, ML 13 mm, TC-44, Stn. 32, 07°31.5′N, 144°50.2′W, 17 July 1969, 50 m. 1 specimen, ML 12 mm, TC-44, Stn. 54, 00°01.8′N, 145°08.8′W, 28 July 1969, 50 m. 4 specimens, ML 6-11 mm, TC-47, Stn. 16, 12°02′N, 144°54′W, 23 January 1970, 50 m. 3 specimens, ML 7-10 mm, TC-48, Stn. 16, 11°45′N, 144°46′W, 2-3 April 1970, 20 m. 1 female, ML 40+ mm, TC-48, Stn. 19, 11°34′N, 144°54′W, 3-4 April 1970, 50 m.

Description: The mantle is muscular except for the thin-walled posterior end (tail) consisting of a gelatinous alveolar material. The mantle is widest (MWI 29.1-*32.4*-34.1) at the anterior edge and tapers into a blunt end. The anterior ventral margin is slightly excavated forming low, pointed lateral angles on each side. The dorsal margin is extended anteriorly into a median rounded lobe.

The fins are wider (FWI 62.1-*69.5*-73.2) than their lengths (FLI 52.0-*59.0*-64.0). They are attached anteriorly at about the midpoint of the mantle length. The anterior margin of each fin forms a rounded lobe. The lateral angles (72°) of the fins are rounded. The posterior margins are straight and are fused to the mantle separately, except for a point (difficult to see) near the tip of the mantle where they join.

The funnel is large, triangular, and has a broad base. The funnel-mantle locking cartilage is straight, the ends are rounded but the anterior end is slightly narrower; the median groove is shallow. The funnel organ of the holotype is large (9 mm long). The dorsal pad has an inverted V-shape with a slender papilla anteriorly and with prominent ridges on the limbs; each limb is about 2.5 mm wide. The ventral pads are oval and elongated (7 mm long, 3 mm wide).

The head is nearly square in cross section and narrower than the mantle (HWI 21.8-*26.0*-29.3). The funnel groove has a distinct edge on each side. The edges continue posteriorly to form the first pair of nuchal folds which bears the small olfactory papillae. The second and third nuchal folds are crescentlike membranes on each side

[2]D = dorsal; V = ventral.

TABLE 1.—Measurements (in millimeters) and counts of *Enoploteuthis obliqua*. TC = RV *Townsend Cromwell*; + = a missing mantle or arm tip, or lost suckers.

Cruise:	TC-48	TC-48	TC-46	TC-44	TC-46	TC-44	TC-44	TC-44
Station:	19	11 (Holotype)	9		9	24	24	18
Sex:	Male	Male	Female	Female[1]	Male	Male	?	?
Mantle length	58	55	50	50	41	37+	20	17
Mantle width	19	16	17	16	14	13	9	9
Head width	17	12	14	12	11	8	5.5	7
Fin length	34	32	31	32	21	17	7	8
Fin width	36	38	36	35	30	22	10	12
Arm length								
Right I	29	25+	25	26	20	17+	9	10
Right II	31+	24	26	27	21	17+	12	11
Right III	28+	26	24	30	20	21+	11	9+
Right IV	31	27+	25	31	20	20+	10	9+
Left IV	32	27	25	31	22	22	10	—
Arm hooks/suckers								
Right I	18/24	20/24	23/26	20/22	20/23	10/18	16/—	18/12
Right II	22/20	21/25	24/24	22/20	20/18	20/—	17/—	18/13
Right III	23/—	22/24	24/20	22/16	21/20	20/—	15/—	17/—
Right IV	28/16	30/21	32/15	31/15	30/14	28/—	18/—	26/—
Left IV	28/16	31/16	31/12	31/19	30/18	29/14	17/—	28/—
Tentacles right/left								
Tentacle length	—	47/53	32/—	45/41	29/30	31/—	12/—	14/—
Club length	—	9+/10	8.5/—	13/13	7/—	7/—	3.5/—	3.5/—
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—	4/4-4/5	4/5-—	4/5-4/5	3/5-4/4	—	—	1/—
Club suckers right/left								
Distal suckers	—	—/13	17/—	14/14	11/—	11/—	—	—
Carpal suckers	—	5/3	5/—	5/5	5/5	4/4	3/4	5/—

[1]From stomach of *Alepisaurus*.

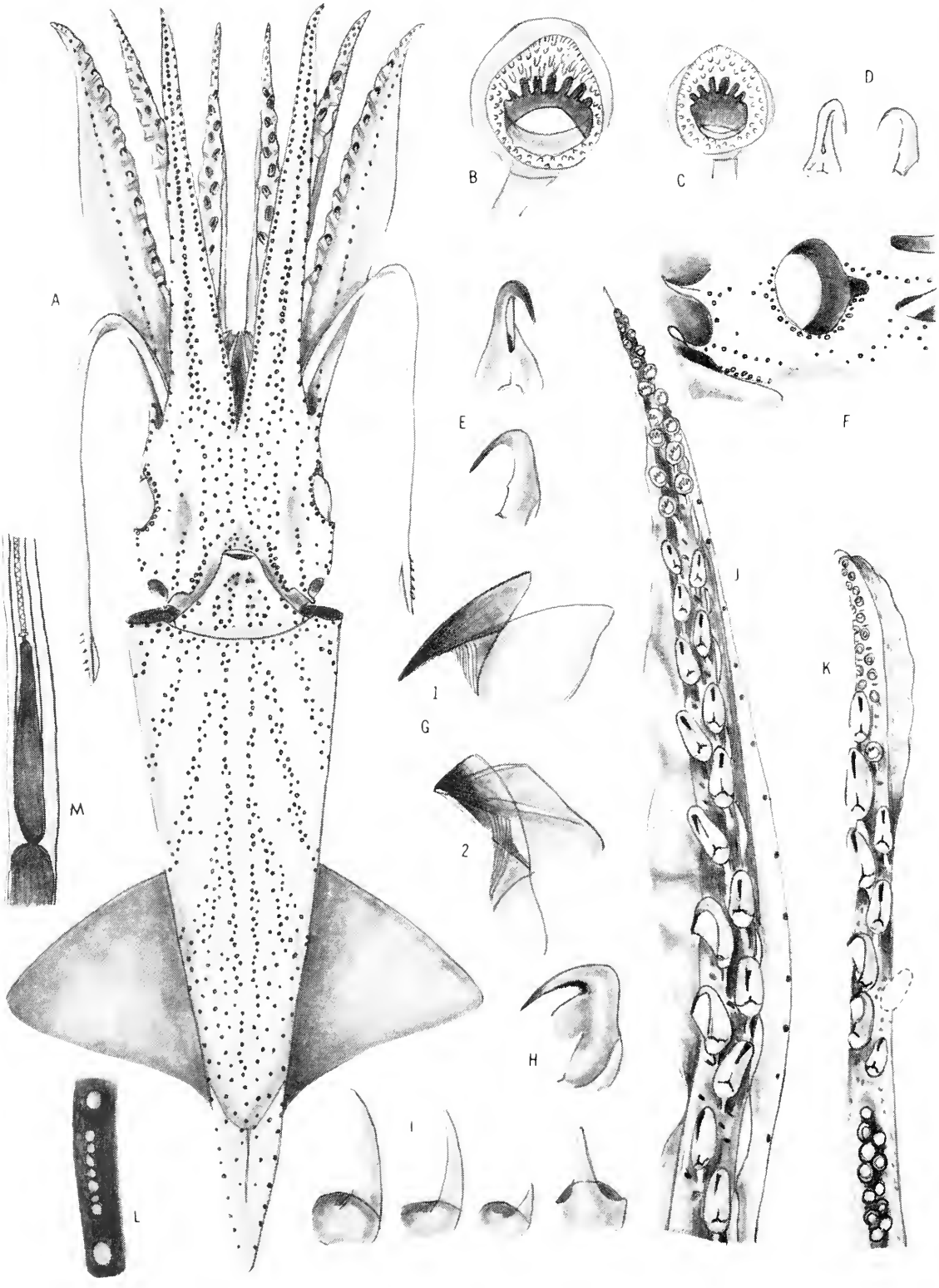
of the neck that are connected to each other posteriorly by a narrow membranous ridge. The third dorsal fold extends dorsally as a membranous ridge, but the ridge does not reach the midline of the head. Dorsal and ventral ocular "windows" are present and the latter easily allows a count of the nine eye photophores on the ventral side of the eyeball. The eye opening is a large, wide, transverse oval with a deep sinus (Fig. 1 F).

The buccal membrane completely hides the buccal mass and surrounding lips. Eight slender supports are joined by slender connectives to the arms in the order DDVD (i.e., all are attached to the dorsal side of the arms except the third pair which are attached to the ventral side of arm III). The inner surface of the buccal membrane is rugose, but without papillae; the lappets are delicate and pointed. The membrane is purple and does not appear much darker than most parts of the body. The chromatophores are small and are scattered evenly on both the supports and the membrane.

The arms are subequal, slender, and much shorter than the mantle length (ALI: I, 48.8-*50.2*-52.0; II, 43.6-*50.2*-54.0; III, 47.3-*51.0*-60.0; IV, 48.8-*53.2*-62.0). They taper gradually to slender tips. The swimming keels are low and poorly developed on the dorsal arms, and they are mainly confined to the distal third of these arms. The swimming keel of arm III is wider than the arm at its greatest width. The lateral membrane or tentacular sheath along arm IV is narrow; it is about half of the arm width proximally and it extends to the tip of the arm. Protective membranes are developed on the ventral side of all arms, but decrease in size in the following order: III, II, I, IV. The dorsal protective membranes on all the arms are low; on arm IV the trabeculae are not evident.

The right ventral arm of the male is hectocotylized. The protective membrane on the medial side of this arm (Fig. 1J) is expanded into an undulating membrane that extends from the eighth pair of hooks to the tip of the arm. The dorsal protective membrane is slightly developed. In the males small tubercles or conical papillae are present between the bases of the hooks and bases of all arms.

All the arms bear two rows of alternating strong hooks, each (Fig. 1E) completely enclosed in a membranous sheath. The distalmost hook is about half the length of the largest one. In both sexes, arm IV has the most hooks. The distal part of each arm is occupied by two rows of suckers with wide apertures and slender stalks. The inner sucker ring bears seven or eight prominent truncated teeth on the distal margin but the proximal margin is smooth (Fig. 1B). The outer ring has numerous pegs (Nixon and Dilly 1977).


A
B
C
D
E
F
G
H
I
J
K
L
M
1
2

The suckers decrease in diameter distally, become globular in shape, and have only three or four blunt teeth.

The tentacles are shorter than the mantle (TLI 62.1-*79.2*-96.4), very delicate and slender. The stalk is laterally compressed, about a third of the width of arm III. The club is not expanded (Fig. 1K). The carpus bears a series of four or five suckers and four, five, or seven pads, and the whole cluster is bordered by a very low ridge on each side. The manus includes a dorsal row of three or four sheathed hooks and a ventral row of four or five slightly larger similarly sheathed hooks (Fig. 1D). These two rows are very close to each other. Marginal suckers are absent. A medial sucker or two may be present in series with the hooks distally. The largest club hook is smaller than any of the arm hooks. The dactylus of the club is occupied by 11 to 17 suckers that are also arranged in two rows. They have long stalks and wide openings. The distal margin of the inner sucker ring bears six or seven slender blunt teeth and the outer sucker ring has numerous pegs (Fig. 1C). Protective membranes are absent. The aboral keel or dorsal membrane is narrow and, at most, about half the length of the club. The tip of the club is rounded and bears a short hoodlike membrane that conceals one or two of the suckers there.

There are two types of light organs on the integument: Large dark ones with pearly white centers and small white ones with very narrow outer pigmented rings. These photophores range in size from small (0.2 mm) to large (0.4 mm), and they are randomly interspersed with each other. The most distinctive feature of this species is the unique arrangement of the mantle photophores. Some of the rows are slanting or oblique (Fig. 1A), instead of the usual straight longitudinal rows described in most other *Enoploteuthis* species. Two median longitudinal rows (two to three photophores in width), separated by an intervening space lacking photophores, extend from the anterior edge of the mantle to the posterior tail. Photophores on the posterior part of the mantle are scattered, those on the anterolateral part are arranged in four oblique rows on each side of the median longitudinal rows. Except for the most posterior row, the oblique rows radiate from the anterior edge of the mantle. The edge of the mantle is lined by a transverse row in which the photophores are closer to each other ventrally than dorsally. A few isolated photophores are present on the dorsal surface of the mantle, none are present on the surface of the fins. The tail has a single row on each side; a few photophores occur on the ventral side, but none are present on the dorsal side.

Six groups of photophores occur on the funnel: Two broad rows separated by a narrow midline space on the ventral side; a short row of six or seven light organs on each lateral margin (one or two photophores are present in the space between these rows posteriorly); and a group of photophores on each side of the bridles on the dorsal side of the funnel.

There are two patches of light organs, separated by a narrow space, in the apical region of the funnel groove. Six rows are recognizable on the ventral surface of the head, three rows on each side of a narrow midline space devoid of photophores. A row (two or three closely set photophores in width) along the lateral edge of the funnel groove extends anteriorly with increased numbers of photophores medial to each eye. It then bifurcates into two branches: one branch extends along the ventral aboral border of arm IV to a point opposite the last arm hook, the other branch continues distally along the base of the tentacular sheath to the tip of arm IV. The next lateral row of the head photophores extends from near the first nuchal fold anteriorly, although a short gap occurs opposite the lens of the eye at the ventral window, along the head and onto the edge of the tentacular sheath where it continues to near the tip of arm IV. The lateralmost row of the head extends from between the second nuchal fold to the posterior margin of the eye; it continues as a single row of closely set photophores along the edge of the eyelid ventrally to the ventral edge of the optic sinus (Fig. 1F). The dorsal edge of the eyelid is devoid of light organs. From the dorsal edge of the optic sinus the row proceeds along the base of the swimming keel of arm II almost to the tip of the arm. Some small white photophores occur near

FIGURE 1.—*Enoploteuthis obliqua* (A-F, K, and L from female paratype, ML (mantle length) 50 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Eye and surrounding area; G, Mandibles: upper (1), lower (2), male, ML 37 mm; H, Dorsal arm sucker, ex-*Alepisaurus* female, ML 50 mm; I, Radular teeth, male, ML 37 mm; J, Hectocotylus, male, ML 41 mm; K, Tentacular club; L, Eye light organs; M, Section of spermatophore, male holotype, ML 55 mm.

the eye region between the median and lateralmost rows.

Nine light organs occur in a single row on the ventral side of the eyeball (Fig. 1L). The terminal photophores are larger and are separated by a wide space from a row of seven much smaller ones that lie adjacent to one another.

The teeth of the radula are long and slender (Fig. 1I); the rachidian has distinct cusps on each side. The first lateral teeth are the shortest.

The mandibles of a young male (ML 40 mm) have distinct growth lines on the wings. The rostrum is heavily pigmented; the edges are sharp and the tip of the upper mandible is very pointed (Fig. $1G_1$). The gular plate of the lower mandible is strengthened by three stout ribs (Fig. $1G_2$).

The gladius has a strong rachis which is rounded anteriorly and thickened medially. The thin vanes are widest at about the midpoint of the total length. The rounded posterior cone is shallow and thin.

A single spermatophore was found in the spermatophoric sac of the holotype (ML 55 mm), and its measurements are given below:

Spermatophore segment	*Length (mm)*
Entire spermatophore	11.5
Spiral filament	4.5
Cement body	1.5
Sperm reservoir	5.5

The spiral filament is slightly sculptured at the aboral end by some irregular ridges. The cement body has a small collar at the oral end (Fig. 1M). A few spiral turns are visible behind the spermatophore cap.

Young individuals: Small specimens (ML 6.0-20.0 mm) are easily separated from other species of *Enoploteuthis* by the unique oblique rows of photophores on the mantle. Early development of the oblique rows are shown in Figure 2Aa and b in specimens ML 7 and 9 mm, respectively. Arm hooks are formed early; six to nine hooks are already present in the arms at ML 6.0 mm. But tentacular hooks appear much later; a ML 17 mm specimen has one tentacular hook and another (ML 20 mm) has none at all. Only two rows of suckers are present on the club.

Remarks: A female specimen tentatively assigned to this species (from the stomach contents of an *Alepisaurus*) exhibits certain features not observed in other specimens of the same or nearly the same size. The arm and tentacular hooks have flattened processes (Fig. 1H). Furthermore, this specimen shows a slight variation in the arrangement of photophores: some photophores occur on the median space of the mantle.

The closest species to *E. obliqua* is *E. leptura* (Leach 1817) from the Atlantic. Both *obliqua* and *leptura* have slender tentacles and clubs. There are few suckers (<20) arranged in two rows on their clubs. However, *obliqua* has fewer tentacular hooks (at most 9) while *leptura* has more (6-12). The carpal cluster is elongate and without prominent ridges in both species. Their spermatophores show similar characteristics: very little sculpture in the spiral filament and one small collar on the cement body.

The specific name *obliqua* reflects the arrangement of the mantle photophores. The oblique arrangement of light organs on the mantle was described earlier by Okutani (1974). His three immature specimens (ML 23.8-25.8 mm) from the EASTROPAC collection and a fourth specimen from the invertebrate collection of the Scripps Institution of Oceanography are all referable to *E. obliqua*. His material was collected in the eastern Pacific.

Distribution: Equatorial regions of the central and eastern Pacific.

Enoploteuthis octolineata n. sp.
(Figs. 3, 2C; Table 2)

Holotype: Female, ML 71 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m, USNM 577607.

Paratypes: 1 female, ML 75 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m, USNM 729721. 1 female, ML 56 mm, TC-46, Stn. 37, 03°23′N, 145°04′W, 26 October 1969, 50 m, USNM 729720. 1 male, ML 46 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m, USNM 729708.

Other material: 1 specimen, ML 10 mm, HMS-47, Stn. 51, 00°44′S, 149°46′W, 2 November 1958, 576 m. 1 specimen, ML 25 mm, HMS-47, Stn. 58, 02°56′N, 150°03′W, 4 November 1958, 212 m. 1 specimen, ML 15 mm, CHG-89, Stn. 5, 02°40′N, 157°31′W, 28 July 1966, 120-240 m. 1 specimen, ML 15 mm, TC-43, Stn. 12, 12°11′N,

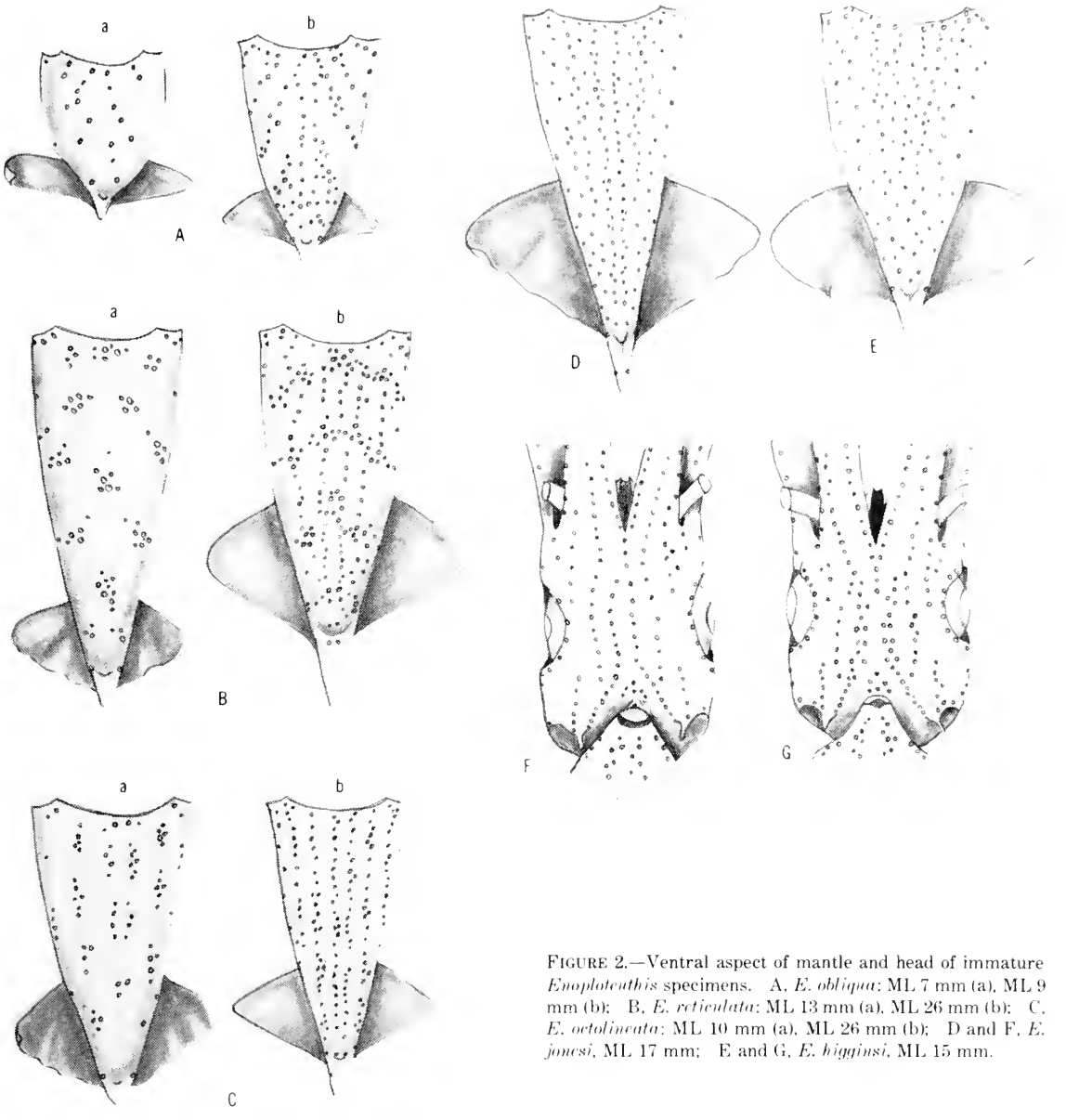


FIGURE 2.—Ventral aspect of mantle and head of immature *Enoploteuthis* specimens. A, *E. obliqua*: ML 7 mm (a), ML 9 mm (b); B, *E. reticulata*: ML 13 mm (a), ML 26 mm (b); C, *E. octolineata*: ML 10 mm (a), ML 26 mm (b); D and F, *E. jonesi*, ML 17 mm; E and G, *E. higginsi*, ML 15 mm.

145°11′W, 9 May 1969, 20 m. 1 specimen, ML 20 mm, TC-43, Stn. 26, 07°33′N, 144°50′W, 15 May 1969, 50 m. 3 specimens, ML 19-30 mm, TC-43, Stn. 38, 03°30′N, 145°06′W, 20 May 1969, 50 m. 2 specimens, ML 21 and 40 mm, TC-43, Stn. 42, 03°32′N, 144°59′W, 22 May 1969, 50 m. 1 specimen, ML 24 mm, TC-43, Stn. 48, 00°04′N, 145°07′W, 26 May 1969, 50 m. 2 specimens, ML 20 and 22 mm, TC-43, Stn. 52, 00°01′N, 145°03′W, 28 May 1969, 50 m. 1 specimen, ML 26 mm, TC-44, Stn. 26, 07°14.8′N, 144°58.8′W, 14 July 1969, 20 m. 1 specimen (from *Alepisaurus* stomach contents), ML 28 mm, TC-44, Stn. 44, 03°49.9′N, 145°18′W, 22 July 1969, 50 m. 1 specimen, ML 20 mm, TC-44, Stn. 56, 00°15.2′N, 144°43.9′W, 29 July 1969, 50 m. 1 specimen, ML 25 mm, TC-44, Stn. 68, 03°39′S, 144°54.5′W, 3 August 1969, 75 m. 1 specimen, ML 36 mm, TC-46, Stn. 41, 03°19′N, 145°03′W, 28 October 1969, 50 m. 2 specimens, ML 14 mm, TC-46,

TABLE 2.—Measurements (in millimeters) and counts of *Enoploteuthis octolineata*. HMS = RV *Hugh M. Smith*; TC = RV *Townsend Cromwell*; + = missing arm tips and lost suckers.

Cruise:	HMS-47	TC-43	TC-46	TC-48	TC-48	TC-44	HMS-47	TC-43
Station:	58	52	37	50	92	26	58	12
Sex:	(Holotype) Female	Female	Female	Male	?	?	?	?
Mantle length	71	75	56	46	33	26	25	15
Mantle width	26	27	21	18	13	11	13	6
Head width	24	21	16	14	10	10	12	5
Fin length	50	52	38	30	19	15	15	7
Fin width	54	56	42	32	23	20	20	8
Arm length								
Right I	43	49	28+	32	23	16	15	8
Right II	42	46	32	[1]32	24	16	18	8
Right III	42	50	31	38	25	18	17	7
Right IV	42	52	38	33	25	16	16	9
Left IV	45	54	35	31	25	18	16	—
Arm hooks/suckers								
Right I	21/36	23/26	20/23+	20/—	—	21/25	16/14	16/12
Right II	22/32	22/24	21/21	18/—	22/—	22/22	21/—	16/14
Right III	25/27	24/28	22/22	21/18	20/—	21/24	23/—	15/11
Right IV	29/25	34/38	32/25	29/23	28/10+	30/22	21/—	18/10
Left IV	30/30	32/34	31/26	29/20+	26/12	29/27	29/12	—
Tentacles right/left								
Tentacle length	75/80	70/70	53/—	43/44	39/37	15/16	25/—	13/—
Club length	19/18	—	14/15	12/13	10/9	5/5	5/—	4/—
Club hooks (Right (dorsal/ventral)-left (dorsal/ventral)	4/5-4/6	—-6/5	4/6-4/6	5/5-4/6	4/5-—	4/5-4/6	5/5-—	—
Club suckers right/left								
Distal suckers	16/17	—	14/14	14/16	10/—	—/19	—	—
Carpal suckers	3/5	6/4	6/5	5/6	4/—	6/4	3/—	—

[1]Length of left arm.

Stn. 45, 03°29′N, 144°54′W, 30 October 1969, 50 m. 1 female, ML 56 mm, TC-46, Stn. 47, 03°23′ N, 145°04′W, 31 October 1969, 115 m. 2 specimens, ML 16 and 20 mm, TC-47, Stn. 45, 03°28′ N, 144°59′W, 3-4 February 1970, 50 m. 1 specimen, ML 39 mm, TC-48, Stn. 35, 07°18′N, 144° 47′W, 11-12 April 1970, 50 m. 1 female, ML 49 mm, TC-48, Stn. 50, 03°29′N, 144°58′W, 17-18 April 1970, 50 m. 1 specimen, ML 33 mm, TC-48, Stn. 92, 00°08′N, 145°00′W, 28 April 1970, 50 m.

Description: The mantle (MWI 36.0-*37.3*-39.1) is cylindrical and tapers gradually toward the end of the blunt tail. Ventrally the anterior edge of the mantle is only slightly excavated and the lateral angles are pointed and low. The anterior dorsal lobe is rounded and also low.

The fin lengths are more than half of the mantle length (FLI 65.2-*68.0*-70.4) and the combined width of both fins is less than the mantle length (FWI 69.6-*73.9*-76.1). The anterior margins project into rounded lobes near their anterior attachments. The lateral angle (about 70°) is rounded and the posterior margin is slightly convex.

The funnel is large; its length equals its width. The funnel-mantle locking cartilage is simple; its anterior end is slightly narrower and more pointed than the rounder posterior end. The funnel valve is a wide semilunar flap; its anterior edge reaches the edge of the funnel opening.

The head (HWI 28.0-*30.2*-33.8) is narrower than the mantle, almost square in cross section, slightly rounded on the top, and is deeply excavated on its posteroventral surface to form a large funnel groove. The dorsal and ventral ocular "windows" are distinct. The eye opening has a deep sinus (Fig. 3G). Three nuchal folds lie on each side of the head; the closest fold to the funnel bears at its posterior end the tonguelike olfactory papilla. These nuchal folds are united to each other by a narrow posterior membrane, although this membrane does not reach the dorsal midline.

The buccal membrane is purple and the eight supports are joined by connectives to the arms in the order DDVD. The membrane is pigmented more heavily than the supports. The lappets are delicately pointed, and the inner surface of the buccal funnel is very rugose but lacks papillae.

The arms are subequal and shorter than the mantle (ALI: I, 60.6-*65.2*-69.7; II, 57.1-*61.8*-69.6; III, 55.4-*66.0*-82.6; IV, 59.2-*66.7*-72.0). They are nearly square at their bases and taper into fine points. Arms I and II have very low keels; arm I is keeled to about half its length and arm II to

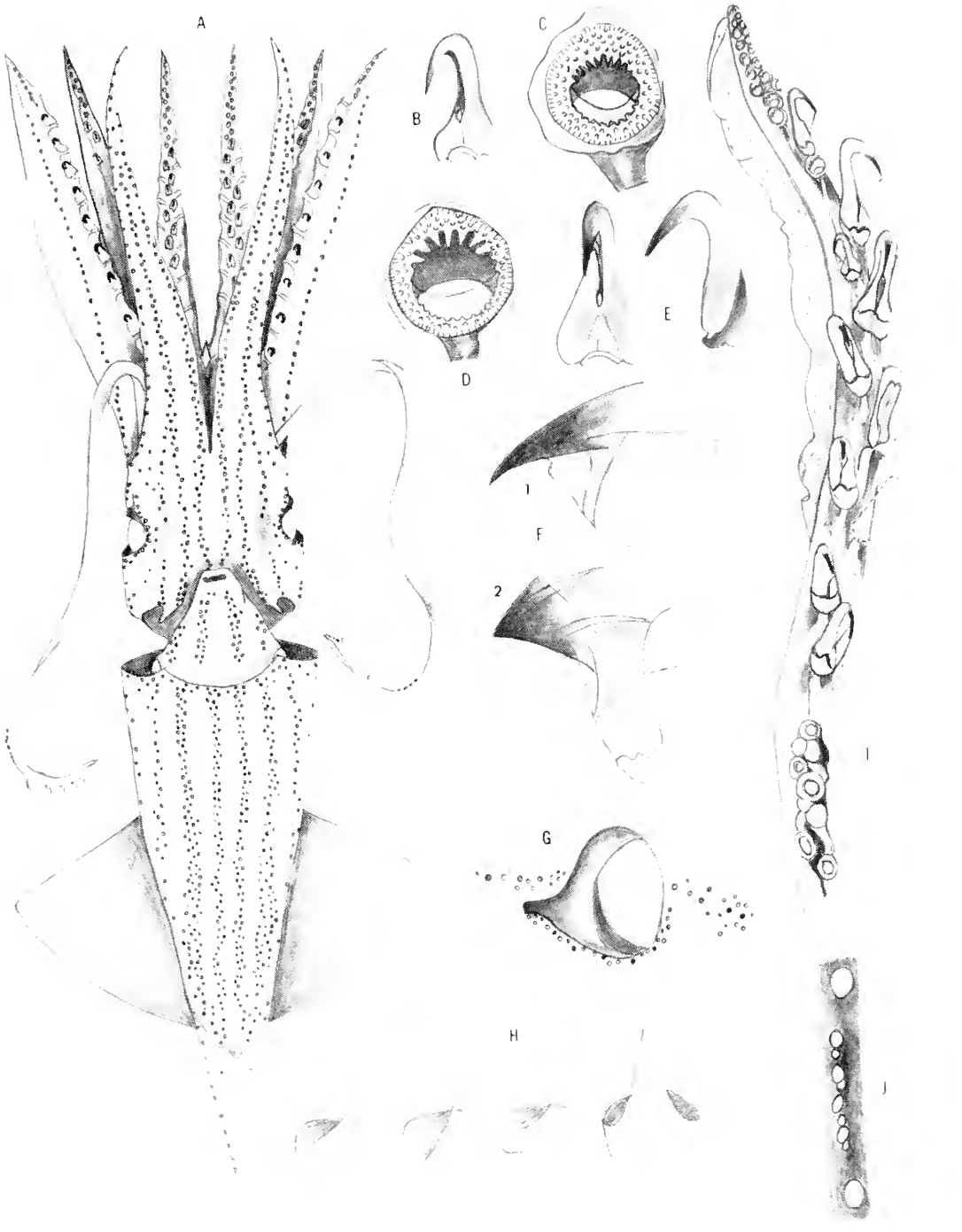


FIGURE 3.—*Enoploteuthis octolineata*. (A-E, G, I, and J from female paratype, ML (mantle length) 75 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Tentacular hook; C, Tentacular sucker; D, Dorsal arm sucker; E, Dorsal arm hook, oral and lateral aspects; F, Mandibles: upper (1), lower (2), male, ML 25 mm; G, Eye and surrounding area; H, Radular teeth, ML 25 mm; I, Tentacular club; J, Eye light organs.

about one-third. The swimming keel of arm III is about as wide as the arm. The tentacular sheath is narrow, about half the width of arm IV near the base. The dorsal and ventral protective membranes are developed on all the arms and extend to the arm tips. The ventral membranes are wider on arm III, although they do not reach the top of the hooks. The protective membranes of arm IV are very narrow, except those on the hectocotylus of the male.

The ventral protective membrane of right arm IV (hectocotylus) of the immature male paratype (ML 46 mm) is slightly enlarged into a narrow undulating membrane, about 1 mm wide, opposite the eighth and ninth pairs of hooks. The dorsal protective membrane is very narrow.

The arm hooks (Fig. 3E) are biserial and are completely covered by sheaths. Arm IV is slightly longer than the other arms, and has the greatest number of hooks. The suckers on the distal part of the arms can be separated into two types. The distalmost suckers are markedly reduced in size, are globular in shape with small apertures, and lack teeth. The proximal suckers have long stalks and wide openings. The inner rings of these suckers have eight to nine large pointed teeth distally, very irregular, smaller teeth proximally, and a wide shelf at the bottom half. The outer ring bears numerous pegs (Fig. 3D).

The tentacles are weakly developed, about as long as the mantle (TLI 93.3-*98.4*-112.7) and very narrow (only about one-third of the width of arm III). The cross section is almost triangular. The club is also narrow (Fig. 3I). The aboral keel extends from opposite the second hook to the tip of the club. Protective membranes are absent, but a short hoodlike membrane is present at the blunt tip. The carpal cluster is composed of a series of three to six smooth-ringed suckers and three to five rounded pads which are biserially arranged in an elongate patch. One of the paratypes (ML 75 mm) has two additional suckers on the stalk located a short distance from the right carpal cluster (such suckers not present in other specimens); corresponding pads, if any, were not seen on the opposite tentacle due to damage. The manus has a total of 9 to 11 sheathed hooks and an occasional sucker in the distal part. These alternating dorsal and ventral hooks are only slightly separated medially. Hooks on the dorsal row are smaller. The hooks (Fig. 3B) resemble the arm hooks in structure, except for the relatively narrower bases of club hooks and their relatively smaller size. The few (16 or 17) distal suckers on the dactylus are also biserial. They have long stalks and wide openings; the inner rings have about 10 sharp teeth distally, a series of smaller denticulations proximally, and an inner shelf at the proximal bottom part (Fig. 3C). The outer ring bears pegs.

There are two types of skin photophores: Very dark ones with whitish centers and white ones with very thin outer black rings (in preservation). The smallest is about half the size of the largest, but intermediate sizes occur. Both types appear randomly interspersed. On the ventral side of the mantle there are eight distinct rows separated by spaces wider than the rows themselves. A continuous midline space is present from the anterior of the mantle to the tail (Fig. 3A). Four parallel rows of varying widths lie on either side of this space. The first and second lateral rows extend from the excavated part of the mantle to the tail. The third row extends from opposite the lateral angle of the mantle to the tip of the mantle, occurring along the lateral margins of the tail as a single row of evenly spaced photophores. The photophores of these rows tend to disperse at the posterior end, particularly the second row, and the rows become slightly intermingled, but each row remains recognizable. The fourth or lateralmost row is composed of widely spaced light organs forming a single line that becomes somewhat irregular opposite the region of the fins. Small photophores are dispersed on the dorsal side of the mantle, but there are none on the fins or on most of the tail except for the lateral row mentioned above and a few very small ones ventrally. A transverse row that has fewer and more widely separated photophores dorsally runs along the edge of the mantle.

Four narrow rows of photophores separated by wide spaces are present on the ventral half of the funnel. There are two additional rows on the dorsal side, one on each side of the bridles.

There are eight separate rows of photophores on the ventral half of the head, four rows on each side of a wide median space. The first row lateral to the midline space originates anterior to the bridle within the apex of the funnel groove and continues directly to the ventral aboral side of arm IV and ends just beyond the distalmost arm hook. The second lateral row begins at the posterior end of the funnel groove and runs along the edge of the groove, over the ventral part of the head, and proceeds anteriorly along the base of

the tentacular sheath to the tip of arm IV. The third row extends anteriorly from the base of the first nuchal fold but is interrupted by the window of the eye, and subsequently divides. One branch unites with the second row at a short distance from the base of the ventral arm. The other branch continues laterally along the edge of the tentacular sheath to the tip of arm IV. The fourth row begins opposite the second nuchal fold and proceeds to the posterior margin of the eye opening and runs along the edge of the eyelid ventrally to the optic sinus (Fig. 3G). The dorsal half of the eyelid has no light organs. From the upper edge of the optic sinus the fourth row continues along the base of the swimming keel of arm III to almost opposite the last arm hook. An additional short arc-shaped row of very small white photophores, set far apart, lies between the third and fourth rows on the posteroventral eye region. This short row is inconspicuous and can easily escape detection.

The light organs on the eyeball vary from 9 to 10. The large terminal photophores are separated by a space from a series of eight or seven adjacent round to oval smaller light organs (Fig. 3J) of varying dimensions.

The radula has seven long, slender, slightly curved teeth in each transverse row. The rachidian tooth has pointed cusps, one on each side. The lateralmost teeth are longest (Fig. 3H).

The mandibles are strong and heavily pigmented. The rostrum of the upper mandible is very pointed and the edges are sharp (Fig. $3F_1$). The lower mandible has three distinct ridges (Fig. $3F_2$). In a specimen ML 25 mm the wings of both halves are transparent.

The gladius is featherlike and the rachis is thickened into a rounded ridge dorsally. The vanes are fragile and narrow. The cone is thin and narrow, but rounded posteriorly. The thickened edge of the vanes described by Roper (1966, fig. 14) in *E. anapsis* is only slightly indicated here.

There are no spermatophores in the largest male paratype (ML 46 mm). The hectocotylus is not fully developed; the lappet is only 1 mm wide and there are no tubercles on the inner surface of the arms. Numerous sperm reservoirs are present in one of the females (ML 75 mm). These are about 6 mm long and are attached in two areas: on the inner wall of the mantle (opposite the midpart of each funnel retractor muscle) and in the concave inner wall of the retractor muscles themselves. The same female is gravid; the diameter of an egg taken from the ovary is slightly <1 mm.

Young individuals: Immature specimens (ML 10-30 mm) have six to eight rows of light organs on the mantle. These rows first appear as a series of elongate patches of large photophores separated by spaces which later develop smaller photophores (Figs. 2Ca, b). At ML 10 mm, all the arms have hooks. The club has two rows of suckers and no hooks. Five of the suckers are set apart proximally and presumably become carpal suckers. At ML 15 mm there are three hooks on the club; by ML 20 mm the club has eight hooks. The tentacles of these immature individuals are shorter than the mantle (TLI 50.0-*68.4*-86.7). The light organs of the eye do not develop simultaneously: some of the smaller individuals have only seven or eight (the two terminal photophores and five or six inner ones).

Remarks: The most distinctive feature of this species is the eight well-defined rows of photophores, separated by wide spaces, on the mantle. In some respects this species resembles *E. leptura* in the shape of the fins and the structure of the clubs and tentacles. However, the latter species has only seven rows of photophores on the mantle, one of which arises from either of the most median pair of rows and does not reach the mantle. This feature is also found in juveniles. The arrangement of the photophores on the head also differs. The third lateral row is unbranched in *E. leptura*.

Distribution: Central Pacific, equatorial waters. Based on sampling for the present collection, *E. octolineata* does not seem to occur in the Hawaiian area.

Enoploteuthis jonesi n. sp.
(Figs. 4, 2D, F; Table 3)

Holotype: Male, ML 47 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 729717.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 24, 14°55.1′S, 164°02′W, 10 February 1966, 90-130 m, USNM 729699. 1 female, ML 82 mm, TC-7, Stn. 12, off Milolii, Hawaii, 16 August 1964, 9-13 m, USNM 577608. 1 female, ML 40 mm, TC-32, Stn. 28, 20°58.6′N, 158°33.7′W, 25 July 1967, 92-122 m, USNM 729707.

Other material: 1 male, ML 27 mm, CHG-89, Stn. 14, 06°06.9′S, 157°44.2′W, 3 February 1966, 70-80 m. 1 specimen, ML 22 mm, CHG-89, Stn. 29, 04°05′S, 167°51′W, 14 February 1966, 120-135 m. 1 specimen, ML 17 mm, CHG-89, Stn. 31, 01°01′S, 168°06′W, 15 February 1966, 90-150 m. 1 specimen, ML 11 mm, TC-32, Stn. 37, 20°59.1′N, 158°12.7′W, 15 August 1967, 55-123 m. 1 female, ML 30 mm, TC-32, Stn. 39, 20°59.6′N, 158°29.3′W, 15 August 1967, 63-101 m. 1 female, ML 35 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m.

Description: The mantle is long, cylindrical, and narrow (MWI 24.4-*34.3*-40.7). The width at the edge is only slightly greater than that at the middle and the sides taper into a blunt tail. The mantle is muscular except for the tail which is thin-walled and translucent, yet very firm. The ventral anterior excavation of the mantle is shallow and the lateral angles and middorsal projection are low and blunt.

Each fin is triangular and their combined width is about three-fifths to four-fifths of the mantle length (FWI 65.9-*74.0*-80.0). The fins are shorter than their combined width (FLI 62.9-*67.5*-70.0). The anterior margin is rounded and the posterior margin is slightly concave. The lateral angles are sharp, about 75°.

The funnel is triangular with a broad base. The funnel-mantle locking cartilage is simple and typical of the genus. The groove is shallow and it spreads out toward the more rounded posterior end of the cartilage. The funnel organ is large; the dorsal pad has a papilla and well-developed ridges; the ventral pads are oval with pointed anterior ends. The semilunar funnel valve is wide and its anteriormost edge does not reach the edge of the funnel opening.

The head is nearly square in cross section, as long as it is wide, and nearly as broad as the mantle (HWI 25.6-*30.9*-37.5). Both dorsal and ventral ocular "windows" are distinct. The eye opening is a wide oval (triangular when constricted) and has a moderately deep sinus. The three crescentic nuchal folds are prominent. The olfactory papilla is tonguelike and arises from the nuchal fold nearest to the funnel. The funnel groove is moderately deep and the sides of this excavation are steep.

The buccal funnel has eight stout supports connected to the arms in the order DDVD. The lappets are pointed; the inner wall of the buccal membrane is very rugose and carries papillae. Both membrane and supports are covered with small fine chromatophores, but the membrane appears darker.

The arms are of moderate length (ALI: I, 40.0-*45.4*-50.0; II, 43.9-*48.8*-51.9; III, 47.6-*51.3*-59.2;

TABLE 3.—Measurements (in millimeters) and counts of *Enoploteuthis jonesi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = lost suckers.

Cruise:	TC-7	TC-7	TC-32	CHG-89	TC-32	CHG-89	CHG-89	CHG-89
Station:	12	12 (Holotype)	28	24	39	14	29	31
Sex:	Female	Male	Female	Male	Female	Male	?	?
Mantle length	82	47	40	35	30	27	22	17
Mantle width	20	14	15	13	11	11	10	9
Head width	21	13	15	11	9	9	8	6.5
Fin length	56	32	28	23	21	17	14	10.5
Fin width	54	34	32	25	24	20	18	14
Arm length								
Right I	35	23	16	15	15	13	[1]9	8
Right II	36	24	19	17	15	14	11.5	9
Right III	39	23	20	17	16	16	12	10
Right IV	46	28	22	20	15	15	13	11
Left IV	46	28	21	19	15	15	—	—
Arm hooks/suckers								
Right I	26/41	20/48	21/—	19/30	17/22	14/18	[1]15/16	11/19
Right II	27/32	23/38	22/—	16/20	18/18	18/18	17/18	14/14
Right III	28/36	21/28	22/—	22/22	17/15	20/18	18/16	14/21
Right IV	31/15	21/10	23/—	25/9	21/15	21/21	19/—	22/20
Left IV	31/22	28/38	25/—	26/16	21/18	21/12+	19/—	—
Tentacles right/left								
Tentacle length	—/86	61/—	65/68	43/—	51/46	48/51	42/42	23/27
Club length	—/20	15/—	15/15	12/—	11/11	11/11	9/9	7/7
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—-7/7	7/7-—	6/7-6/7	7/6-—	7/7-6/7	—-7/6	7/7-—	6/6-5/7
Club suckers right/left								
Distal suckers	—/68	64/—	72/52+	70	64/72	—/64	72/—	68/64
Carpal suckers	—/4	4/—	3/4	4/—	3/4	—/4	3/—	4/4

[1]Length or count of left arm.

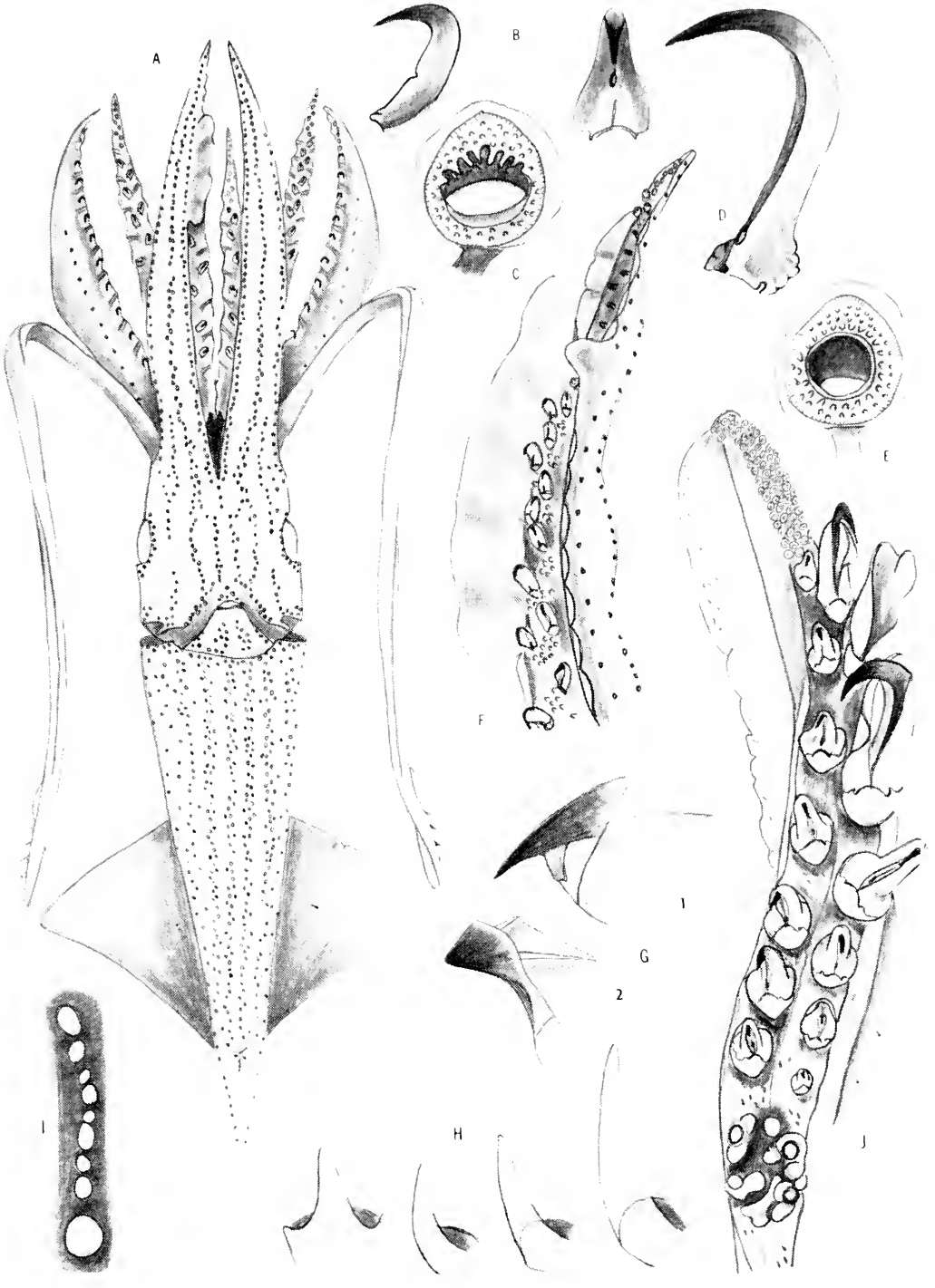


FIGURE 4.—*Enoploteuthis jonesi.* (A-F, I, and J from male holotype, ML (mantle length) 47 m; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm hook, oral and lateral aspects; C, Dorsal arm sucker; D, Tentacular hook; E, Tentacular sucker; F, Hectocotylus; G, Mandibles: upper (1), lower (2), ML 27 mm; H, Radular teeth, ML 27 mm; I, Eye light organs; J, Tentacular club.

IV, 50.0-*55.0*-59.6). Arm IV is longest in both sexes. The arms are nearly square in cross section and they taper distally into fine delicate tips. The keels of arms I and II are confined mainly to the distal halves of the arms. The swimming keel of arm III is as wide as the arm at its midpoint. The lateral membrane (or tentacular sheath) of arm IV is moderately wide and extends to the tip of the arm. Dorsal and ventral protective membranes are present in all the arms. The ventral membrane is more developed than the dorsal, particularly on arm III.

In the males the right arm IV is hectocotylized. The ventral protective membrane on this arm forms a very wide lappet that extends from about the middle half, opposite the sixth pair of hooks, to about four-fifths of the arm length. Distally the membrane is much narrower and tapers to the arm tip (Fig. 4F). The dorsal protective membrane is slightly modified: a small tongue-like flap is developed opposite the distal end of the larger medial lappet. In addition, the males have numerous conical tubercles at the bases of the oral surface of all the arms and between the bases of all the hooks.

The biserial and regularly arranged hooks are completely sheathed by membranes (Fig. 4B). The distal arm suckers have long stalks. Each inner ring has eight teeth on its distal half and none on the smooth proximal half (Fig. 4C). The outer rings bear pegs all around. The suckers are progressively smaller distally; the distal suckers assume a globular shape, have small apertures, no teeth, and no outer rings.

The tentacles are longer than the mantle (TLI 104.9-*153.3*-188.9) and are about twice the length of the longest arm. The stalk is oblong in cross section near the base, very muscular, and almost as thick as arm III. The proximal part of the club is as narrow as the stalk or only slightly expanded. The club becomes unusually narrow in the distal one-third (Fig. 4J). The tip is blunt. The aboral keel is about one-half of the club length. A semilunar membrane is present on the ventral or oral side; it extends between the carpal area and the fourth pair of hooks. Protective membranes are developed on the ventral side but are rudimentary dorsally. Protective membranes are absent on the dactylus. The carpal cluster consists of three or four smooth-ringed suckers and several rounded pads in a compact round cluster together with some irregular grooves and ridges. There are 13 or 14 robust hooks in two rows on the club. The ventral row includes a series of greatly enlarged hooks. The hooks (Fig. 4D) are enclosed by membranes but the tips are exposed. These hooks have very broad bases and are set in rounded shallow excavations. Marginal suckers are absent. Twelve to 18 transverse rows of 4 small suckers per row occupy the narrow dactylus. About 12 of these suckers at the tip are slightly larger than the immediately preceding transverse row, thus forming a cluster at the tip of the club. All the club suckers have smooth inner rings (Fig. 4E). The pegs on the outer ring are moderately long and may hide the smooth edge of the inner ring from view.

The integumentary photophores occur in different sizes ranging from about 0.2 to 0.4 mm. A photophore may appear dark or very pale, depending on the extent of pigmentation. Many of the larger photophores are heavily pigmented, except for a small central area. Most of the smaller photophores are pale because pigmentation is confined to the periphery in the form of a very thin dark ring. Intermediate conditions between these extremes occur. At first glance the photophores on the mantle appear scattered at random, but on closer examination one can recognize four multiserial, ill-defined rows: two rows on each side of a very narrow midline space that extends from the anterior opening of the mantle to the tail and bounded laterally by a broad zone of photophores (Fig. 4A). Each row consists of large and small photophores set near each other; smaller and whiter ones occupy the central part of the row, while the larger and more conspicuously darker ones are located mostly on the outer area of the row. These rows become more difficult to distinguish posteriorly. A single row of evenly spaced photophores extends along the lateral margins of the tail. Numerous photophores occupy the ventrolateral surface and some single photophores, generally small ones, are scattered on the dorsal surface of the mantle, except near the midline. The edge of the mantle is lined by a single row of photophores; the photophores are spaced progressively farther apart toward the dorsal midline.

The funnel has six groups of photophores: Two rows separated by a midline space on the ventral side; a short row on each lateral side; and two dorsal rows, one on each side of the bridle.

A small triangular cluster of photophores is situated in the apex of the funnel groove. A space in the ventral midline of the head is broken by a

short row of two or three photophores that bifurcates at the fork of the ventral arms; each branch continues along the ventral aboral side of arm IV to almost the tip. A row of closely set photophores runs along the edge of the funnel groove and divides near the apex of the groove into two branches, each with photophores in single file. The branches reunite near the base of arm IV. The row continues distally along the base of the tentacular sheath to the tip of the arm. The third lateral row on the head begins anterior to the first nuchal fold, has a gap at the window of the eye, and then continues and splits into two branches: A medial branch that continues anteriorly and ends near the base of arm IV at the midline of the tentacular sheath and a lateral branch that extends along the edge of the tentacular sheath and terminates about the level of the last hook on arm IV. The lateralmost row on the head also starts at the first nuchal fold, continues along the nuchal crest, and turns toward the posterior eyelid where it runs along the ventral edge to the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and stops at about three-fifths of the arm length. The dorsal eyelid lacks photophores.

There are nine irregularly spaced photophores on the ventral part of the eyeball (Fig. 4I). The posteriormost light organ is larger than the anteriormost which in turn is larger than the remaining seven light organs. The latter are slightly different from each other in size and shape.

The teeth of the radula are long (lateralmost teeth are longest), blunt, and slightly curved (Fig. 4H). Of the seven teeth only the rachidian tooth has small lateral cusps.

The upper mandible of a small specimen (ML 30 mm) has distinct growth lines on the wings (Fig. $4G_1$). The riblike ridges on the gular plate of the lower mandible are well developed (Fig. $4G_2$).

The gladius is feather-shaped. The rachis is blunt anteriorly and forms a strong ridge dorsally through its length. The vanes are narrow, widest at about a third of the length of the gladius. The posterior end is curved inward ending in the cone.

The largest female (ML 82 mm) is gravid; the ovaries are distended and extend to the posterior part of the mantle cavity. The eggs are opaque and about 1 mm in diameter.

None of the males have spermatophores.

Young individuals: Immature individuals (ML 11-22 mm) have relatively wider mantles (MWI 45.5-*57.0*-72.7) than adults. At ML 11 mm the arms have the following armature: 1 to 3 suckers proximally, 7 to 12 hooks, and 15 to 20 suckers distally. The tentacles are distinctly longer than the mantle (TLI 172.7). The club has three hooks along with nine biserial suckers on the manus. Two of the suckers are slightly set apart (future carpal suckers). Four rows of minute suckers are located on the dactylus. At ML 17 mm the arms have no proximal suckers, 12 to 18 hooks, and 19 to 21 distal suckers. The club resembles that of the adult, except that two marginal suckers are present on the dorsal distal side of the manus and although there are already four carpal suckers, the carpus is still not completely developed. The photophores on the mantle are not distinctly arranged into rows, except for two medialmost rows which are separated by a narrow space (Fig. 2D). The rows on the head are each composed of photophores in single file (Fig. 2F). The number and position of the rows agree with those of the adult.

Remarks: Adults of this species resemble superficially *E. chuni* Ishikawa 1914 from Japan, but they are easily distinguished by the photophore pattern of the head and arms. *Enoploteuthis chuni* has seven rows of photophores on the head (including the rows passing along the ventral eyelids) (pl. XX, fig. 1, Sasaki 1920), whereas *jonesi* has six rows. There is a distinct midventral multiserial row on the head of *chuni*, whereas the ventral midline of *jonesi* is a clear space, except for two or three single photophores near the fork of the ventral arms anteriorly. Some rows of photophores on the head divide and reunite in *jonesi*, a condition absent in *chuni*. The row of photophores at the base of the swimming keel of arm III reaches the tip of the arm in *chuni*, but in *jonesi*, the same row ends slightly beyond one-half to three-fifths of the arm length. These observations were confirmed by T. Okutani of the Tokai Regional Research Laboratory (presently with the National Science Museum, Tokyo) who kindly examined specimens of *E. chuni* from Suruga Bay and compared them with illustrations of *E. jonesi* sent to him. In addition, there are more distal club suckers in *chuni* (90) than in *jonesi* (64-72) and these suckers are toothed in *chuni* and smooth in *jonesi*.

The counts and measurement of *E. jonesi*

overlap those of *E. anapsis* Roper, 1964 from the tropical Atlantic and Caribbean. These species exhibit the following differences: 1) The midline space on the mantle in *jonesi* continues uninterrupted to the tail, but this space in *anapsis* has some scattered photophores near the tail; 2) the row that traverses the window on the ventral side of the head is bifurcate in *jonesi* whereas it is single in *anapsis*. The tentacles and clubs of *anapsis* are relatively longer than those of *jonesi*. The distal club suckers are more numerous in *jonesi* (64-72) than in *anapsis* (40-50).

This species is named after Everet C. Jones, former fishery biologist at the Honolulu Laboratory. It was under the supervision of E. C. Jones that the specimens collected during some of the cruises reached me in good condition.

Distribution: Central Pacific, Hawaiian waters, and equatorial region.

Enoploteuthis higginisi n. sp.
(Figs. 5, 2E, G; Table 4)

Enoploteuthis species B, Young 1978: figure 9B.

Holotype: Male, ML 37 mm, *Teritu*, Stn. 6 off Waianae, Oahu, September 1969, 110 m, USNM 729710.

Paratypes: 1 male, ML 35 mm, CHG-89, Stn. 11, 06°04.9'S, 157°36.9'W, 2 February 1966, 140-200 m, USNM 729714. 1 female, ML 53 mm, TC-32, Stn. 22, 21°02'N, 158°29.7'W, 21 July 1967, 67-117 m, USNM 729723. 1 female, ML 45 mm, TC-32, Stn. 56, 21°22.4'N, 158° 14.6'W, 23 August 1967, 97-179 m, USNM 577609.

Other material: 1 specimen, ML 27 mm, HMS-47, Stn. 51, 00°44'S, 149°46'W, 2 November 1958, 576 m. 1 specimen, ML 12 mm, CHG-51, Stn. 164, 16°44'N, 169°16'W, 14 February 1961, 100 m. 1 specimen, ML 12 mm, CHG-51, Stn. 172, 19°21'N, 169°20'W, 15 February 1961, 0-100 m. 1 specimen, ML 16 mm, CHG-89, Stn. 29, 04°05'S, 167°51'W, 14 February 1966, 120-135 m. 1 specimen, ML 11 mm, CHG-89, Stn. 30, 02°59'S, 167°51'W, 15 February 1966, 100-125 m. 1 male, ML 46 mm, TC-32, Stn. 23, 21°00.2'N, 158°30.1'W, 22 July 1967, 17-25 m. 1 female, ML 60+ mm, TC-32, Stn. 28, 20°58.6'N, 158°33.7'W, 25 July 1967, 8-60 m. 1 female, ML 30 mm, 2 specimens, ML 12 and 19 mm, TC-32, Stn. 33, 20°58.8'N, 158° 28.4'W, 13 August 1967, 83-99 m. 1 female, ML 32 mm, 1 specimen, ML 22 mm, TC-32, Stn. 37, 20°59.1'N, 158°12.7'W, 15 August 1967, 55-123 m. 1 male, ML 30 mm, 2 females, 37 and 40 mm, TC-32, Stn. 38, 20°58.7'N, 158°27.9'W, 15

TABLE 4.—Measurements (in millimeters) and counts of *Enoploteuthis higginsi*. TC = RV *Townsend Cromwell*; CHG = RV *Charles H. Gilbert*; + = missing mantle tip and lost suckers.

Cruise:	TC-32	TC-32	TC-32	TC-32	*Teritu*	CHG-89	TC-32	CHG-51
Station:	28	22	23	56	6	11	56	172
Sex:	Female	Female	Male	Female	(Holotype) Male	Male	Female	?
Mantle length	60+	53	46	45	37	35	29	22
Mantle width	24	20	18	14	14	13	13	11
Head width	20	17	13	14	15	12	11	10
Fin length	—	39	30	34	27	23	20	15
Fin width	58	42	38	34	30	30	24	21
Arm length								
Right I	42	32	25	26	20	20	[1]13	15
Right II	24	36	27	25	20	21	[1]15	12
Right III	48	33	28	28	21	20	[1]15	12
Right IV	51	37	28	31	23	23	19	11
Left IV	53	34	32	33	23	—	17	13
Arm hooks/suckers								
Right I	26/22	25/34	19/—	25/22	20/16	24/16	16/19	16/20
Right II	29/27	26/34	22/—	25/20	22/16	23/20	17/20	18/20
Right III	32/28	28/33	22/—	25/22	22/20	22/20	18/23	16/21
Right IV	28/28	26/21	25/—	29/20	22/2+	26/14+	22/23	18/6
Left IV	28/26	27/20	27/—	29/22	26/16	—	20/23	20/7
Tentacles right/left								
Tentacle length	—	108/117	110/—	—/92	41/41	60/—	—/48	34/27
Club length	—	17/17	16/—	—/16	11/11	11.5/—	—/9	—
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	—	5/6-5/6	4/6-—	—-6/6	5/6-5/6	5/6-—	—-4/6	—
Club suckers right/left								
Distal suckers	—	68/68	—	—/60	60/60	72/—	—/64	—
Carpal suckers	—	3/3	3/—	—/3	3/2	3/—	—/3	—

[1]Length or count of left arm.

August 1967, 8-25 m. 1 male, ML 46 mm, TC-32, Stn. 41, 20°58.9′N, 158°29.1′W, 16 August 1967, 59-122 m. 1 female, ML 37 mm, TC-32, Stn. 44, 21°00.1′N, 158°29.1′W, 18 August 1967, 72-118 m. 1 female, ML 47 mm, TC-32, Stn. 45, 20°58.1′N, 158°28.7′W, 18 August 1967, 12-31 m. 2 specimens, ML 27 and 28 mm, TC-32, Stn. 46, 20°57.6′N, 158°28.7′W, 18 August 1967, 77-118 m. 1 female, ML 35 mm, TC-32, Stn. 48, 20°59.7′N, 158°27.7′W, 19 August 1967, 60-104 m. 1 female, ML 29 mm, TC-32, Stn. 56, 21°22.4′N, 158°14.6′W, 23 August 1967, 97-179 m.

Description: The muscular mantle is slender (MWI 31.1-*37.9*-44.8) and conical; the translucent tail is slender and ends bluntly. The ventral anterior edge of the mantle is not deeply excavated and the lateral angles are pointed, but low. The dorsal anterior lobe is low.

The fins are triangular, wide (FWI 75.6-*81.2*-85.7), and long (FLI 65.2-*70.4*-75.6). The anterior margin near its attachment is a rounded lobe, but more laterally it appears straight. The lateral angles (about 75°) are rounded at the tip. The slightly concave posterior margins join the mantle independently, but the union of both fins (close to the tip of the mantle) is indistinct.

The funnel is triangular and wide at the base. The funnel valve is a wide semicircular flap. The funnel organ is large; an anterior papilla and thick lateral ridges are present. The funnel-mantle locking cartilage is simple with a shallow groove. The anterior part of the cartilage is slightly narrower than the posterior end.

The head is as wide as the mantle (HWI 28.3-*34.0*-40.5). The eye opening is a wide oval with a deep anterior sinus. The funnel groove is moderately deep and the lateral sides continue posteriorly as sharp ridges. The ventral ocular "windows" are translucent. The three nuchal folds are very prominent. The tongue-shaped olfactory organ is attached to the first fold closest to the funnel. The second and third folds are united to each other posteriorly and the third fold on each side continues as a much reduced fold toward the dorsal midline.

The buccal membrane has a DDVD attachment to the arms. Numerous folds and broad tonguelike papillae occur on the inner surface of the membrane. The external surface is densely supplied with small purplish chromatophores so that it is darker than most parts of the body.

The arms are slender but muscular, nearly square in cross section at the base and finely pointed at their tips. The arms are moderate in length (ALI: I, 44.8-*54.8*-60.4; II, 51.7-*58.0*-67.9; III, 51.7-*58.5*-62.3; IV, 58.6-*65.5*-73.3). Arm IV is longest in both sexes. The swimming keels are developed to about one-half of arm I distally, two-thirds of arm II distally, and complete in arm III where they are as wide as the arm at the mid-section. The lateral membrane (tentacular sheath) of arm IV is wide and reaches to the tip of the arm. Dorsal and ventral protective membranes are developed on all the arms of both sexes. They are widest on arm III and least developed on arm IV, except on the hectocotylized arm of the male.

The right ventral arm of the male is hectocotylized. The protective membranes of this arm are modified. At about the middle half of the arm opposite the sixth pair of hooks, the ventral protective membrane becomes enlarged into a wide undulating flap that is reduced abruptly about three-fourths of the arm length and continues distally to the tip of the arm as a much narrower membrane. The dorsal protective membrane, on the contrary, is only slightly modified. A short semilunar flap is present opposite the distal end of the larger ventral flap (Fig. 5F). Numerous conical papillae are scattered on the oral surface of the arms of males between the bases of the hooks and on the bases of the arms.

The arms have biserial hooks proximally and biserial suckers distally. The hooks (Fig. 5E) are strongly attached and completely enclosed by sheaths. About half of the suckers at the tips of the arms have long stalks and wide openings. The distal half of the inner rim of the sucker has seven to eight teeth; the two middle teeth are narrower than the lateral teeth; a shelf is visible on the proximal half (Fig. 5B). The outer ring bears numerous pegs. The remaining suckers gradually become smaller distally, assuming a globular shape with smaller openings that lack teeth and outer rings.

The robust tentacles are much longer than the mantle (TLI 110.8-*190.3*-239.1). The stalk near the base is almost square in cross section and as stout as arm III. The carpus and manus of the club are wide but the dactylus is quite narrow (Fig. 5G). The carpal cluster is compact and it includes three smooth-ringed suckers (very rarely two suckers) and several rounded pads and some elongate ridges and grooves; these are arranged in an oval cluster. Ten to 12 very robust, sheathed hooks are present in two rows

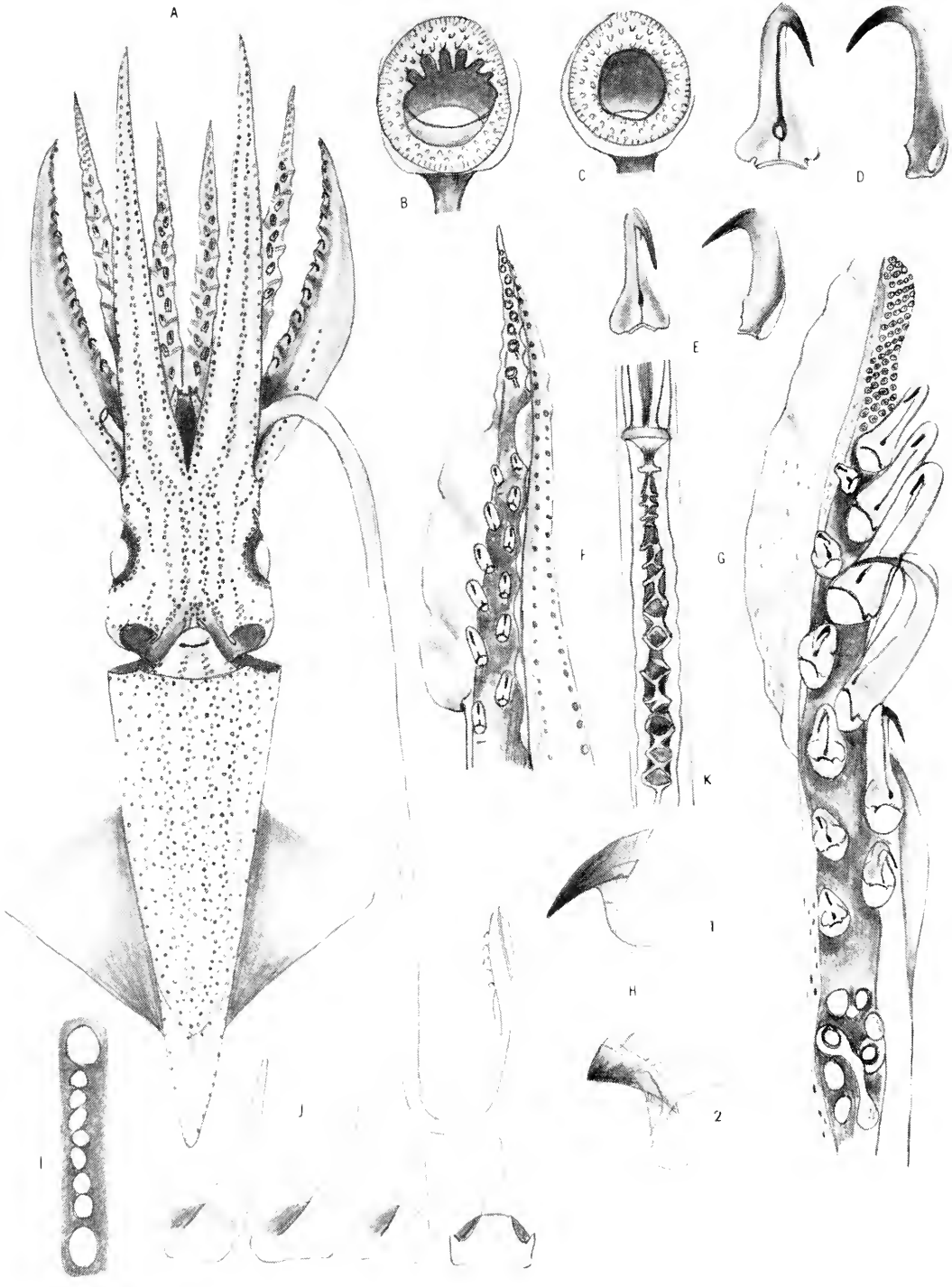


FIGURE 5.—*Enoploteuthis higginsi*. (A-E, G, and I from female paratype, ML (mantle length) 45 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Dorsal arm sucker; C, Tentacular sucker; D, Tentacular hook, oral and lateral aspects; E, Dorsal arm hook, oral and lateral aspects; F, Hectocotylus, male holotype, ML 37 mm; G, Tentacular club; H, Mandibles: upper (1), lower (2), female, ML 37 mm; I, Eye light organs; J, Radular teeth, female, ML 37 mm; K, Section of spermatophore, male, ML 46 mm.

on the manus. The ventral row includes a few large curved hooks, the largest hook is about one-fifth larger than the largest arm hook. The hooks have broad bases (Fig. 5D) and fit into shallow depressions on the club. The distal club suckers are arranged in four longitudinal rows (between 15 and 18 suckers in each row). The inner rings of these suckers are smooth but are surrounded by an outer ring with broad pegs that can be mistaken for teeth of the inner ring (Fig. 5C). A few suckers in the distal part of the dactylus are slightly enlarged and form a cluster there at the blunt end of the club. The dorsal or aboral keel is well developed and extends from opposite the third dorsal hook to the blunt end. A smaller semilunar membrane lies on the oral or ventral side of the club. It extends from opposite the distal half of the carpal cluster to opposite the second or third ventral hook. Protective membranes are poorly developed but recognizable.

The integumentary photophores range in size from about 0.2 mm to about 0.4 mm with varying degrees of pigmentation. Some are very dark with small pearl gray centers, others are lighter with varying widths of peripheral pigmentation. Those with very thin dark rings appear palest or almost white. The photophores on the ventral surface of the mantle appear to be distributed at random (Fig. 5A). They are concentrated on the ventral surface except at the tail and gradually become widely scattered toward the dorsal surface. A single row extends along each lateral margin of the tail. The free edge of the mantle opening is lined by a transverse row where the photophores are farther separated dorsally. There are no photophores on the fins, or on most of the ventral area of the tail.

Two rows of photophores separated by a median space are present on the ventral surface of the funnel. A shorter row or patch occurs on each of the lateral margins and a wider strip is found on each of the dorsolateral surfaces of the funnel.

The distribution of the photophores on the head is rather intricate. A small cluster lies in the apical region of the funnel groove. The ventral midline of the head is not totally clear of light organs, as a few isolated ones may be present. A very short row of three to four photophores in single file on the ventral midline (near the bases of arm IV) splits into two at the fork of the arms; each branch then continues along the ventral aboral edge of arm IV, ending a short distance from the distal tip of the arm. A row of photophores begins near the first nuchal fold, follows the curve of the funnel groove, and at a point near the apex of the funnel groove it splits into a wider medial branch and a narrower lateral branch. These branches reunite near the base of arm IV and the combined row proceeds anteriorly along the base of the tentacular sheath to the tip of arm IV. The next lateral row begins anterior to the first nuchal fold, is interrupted by a gap at the window of the eye, continues for a short distance, and divides into two short branches; each branch then extends to the edge of the tentacular sheath independently. A row of single photophores runs along the edge of the tentacular sheath and stops a short distance from the tip of arm IV. The lateralmost row on the head extends from the first nuchal fold along the nuchal crest, then anteriorly to and along the ventral margin of the eyelid, and ends at the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus, continues along the base of the swimming keel of arm III, and terminates at about one-half the length of the arm. Two or three isolated small photophores occur in the area surrounding the ventral part of the eye opening; one photophore is usually located directly lateral to the window.

There are nine light organs on the ventral part of the eyeball. The terminal organs are much larger and slightly separated from seven smaller, closely set, light organs (Fig. 5I).

The radular teeth (seven teeth in a series) are long and slender. The outermost lateral teeth are longest while the innermost lateral teeth are shortest. The rachidian tooth has cusps. The three median teeth are almost straight while the two outermost lateral teeth are slightly curved (Fig. 5J).

The upper mandible (Fig. $5H_1$) has a pointed rostrum with very sharp edges and the lower mandible (Fig. $5H_2$) has three well-developed ribs on the gular plate.

The gladius is feather shaped and the midrib is low and rounded. The cone is narrow and rounded at the extreme end. The vanes start to broaden at about one-third of the length and reach their greatest width at about half of the length. The lateral edges of the gladius appear slightly thickened when held against a strong light.

Spermatophores from a male (ML 46 mm) are about 14 mm in total length. The cement body is slightly greater than half the length of the sperm reservoir and has two collars at the oral end (Fig.

5K), the anterior much smaller than the posterior. The aboral part of the spiral filament is supplied with numerous intricate diamond-shaped depressions separated by thickened ridges. Two to four turns are present behind the cap. A spermatophore examined has the following measurements:

Spermatophore segment	*Length (mm)*
Entire spermatophore	13.8
Sperm reservoir	5
Cement body	2.8
Spiral filament	6.0

Some eggs taken from the ovary of the female paratype (ML 53 mm) measured about 1.2 mm each.

Young individuals: Small individuals (ML 11-16 mm) have relatively wider mantles (MWI 56.3-59.4-63.6) and the photophores on the mantle are scattered (Fig. 2E) as they are in the adult. At ML 15 mm all the rows of photophores on the head correspond to those of the adult with respect to number and position (Fig. 2G). The most medial row consists of several photophores set close to each other as in the adult. All other rows are composed of a single line of photophores. At ML 12 mm the tentacles are robust and longer than the mantle (TLI 108.3), more than the length of the arm. The club has two carpal suckers, four hooks on the ventral side of the manus among a group of 16 suckers (presumably future hooks), some marginal suckers, and numerous quadriserially arranged suckers on the dactylus. The aboral keel is also developed. The arms bear between 12 and 14 hooks and a sucker at the base of one of the dorsal arms. Thirteen or 14 suckers occupy the distal part of arms I, II, and III, and 24 suckers on arm IV. At ML 16 mm there are still 4 club hooks and 2 carpal suckers, but the arm hooks have increased (18 on arm IV) as have the distal suckers. At ML 19 mm, 16 to 19 hooks are observed on the arms and 6 to 7 on the club along with an increased number of distal arm suckers and club suckers. At this stage three carpal suckers are present as in the adult.

Remarks: The species can be easily confused with *E. jonesi*; counts and measurements overlap and both species can be found in the same trawl hauls. However, a close examination of the material reveals a series of minor but consistent characteristics that separate one from the other even at a small size (ML 10 mm). At comparable sizes the tentacles and clubs are similar in structure, but *jonesi* has 13 or 14 club hooks and usually 4 carpal suckers while *higginsi* has 11 or 12 club hooks and usually 3 carpal suckers. Both have long tentacles, but they are relatively longer in *higginsi*.

Discrete longitudinal arrangement of photophores on the mantle is wanting in *higginsi* while a median space and identifiable rows are found in *jonesi*. The arrangement of photophores on the head also shows some differences: 1) The row closest to the midline is multiserial in *higginsi* whereas it is simple in *jonesi*; 2) isolated photophores occur in the midline area of the head and in the space near the eye in *higginsi* but are absent in *jonesi*; 3) the row directly anterior to the window is bifurcate in both species but in *higginsi* both branches extend to the tentacular sheath whereas in *jonesi* only the lateral branch does; and 4) the row of photophores on arm III is incomplete in both species, but in *higginsi* the row rarely extends more than 50% of the arm length (45-52% of arm length, 11 specimens) and in *jonesi* the row is more than half the arm length (56-85% of arm length, 18 specimens).

Enoploteuthis higginsi, like *E. jonesi*, shares many characteristics with *E. chuni* and *E. anapsis* (see remarks section of *E. jonesi*), but the scattered distribution of photophores on the mantle is distinctive of *higginsi*. Rows do not occur on the mantle in any stage of development in *higginsi*. At ML 10 mm, or smaller, the rows are already evident in *anapsis* (Roper 1966, figs. 22, 23).

Specimens captured in Hawaiian waters which were labeled *Enoploteuthis* sp. B and reported in Young (1978) also belong to this species (R. E. Young[3]).

This enoploteuthid squid is named after Bruce E. Higgins, former fishery biologist at the Honolulu Laboratory under whose leadership most of the material was collected during cruise 32 of the RV *Townsend Cromwell* in Hawaiian waters.

Distribution: Central Pacific, Hawaiian, and equatorial regions.

[3]R. E. Young, Department of Oceanography, University of Hawaii, Honolulu, HI 96822, pers. commun. 3 March 1980.

Enoploteuthis reticulata Rancurel 1970
(Figs. 6, 2B; Table 5)

Enoploteuthis reticulata Rancurel 1970: figures 31-37 (incorrect spelling *reticula* in figures 31-33).
Enoploteuthis sp. (No. 1), Okutani, 1974: figures 12a, b, e.
Enoploteuthis sp. A, Young 1978: figures 9B, 10A.

Material examined: 1 male, ML 130 mm (regurgitated by a porpoise) CHG-7, 20°42.7'N, 157°50'W, 3 February 1953, USNM 729718. 1 male, ML 117 mm, HMS-30, Stn. 3, 28°38.5'N, 161°20.3'W, 16 July 1955, 100 m. 1 specimen, ML 26 mm, TC-7, Stn. 5, off Waianae, Oahu, 12 August 1964, 60-100 m. 1 female, ML 35 mm, TC-32, Stn. 3, 21°22.5'N, 158°13.5'W, 13 July 1967, 15-25 m. 1 specimen, ML 13 mm, TC-32, Stn. 4, 21°20.9'N, 158°13.1'W, 13 July 1967, 75-107 m. 1 specimen, ML 18 mm, TC-32, Stn. 6, 21°21.7'N, 158°13.3'W, 14 July 1967, 83-124 m. 1 female, ML 45 mm, TC-32, Stn. 9, 21°21.5'N, 158°13.5'W, 15 July 1967, 17-25 M. 2 females, ML 39 and 62 mm, TC-32, Stn. 15, 21°20.3'N, 158°12.2'W, 17 July 1967, 16-30 m, USNM 729691. 1 specimen, ML 30 mm, TC-32, Stn. 28, 20°58.6'N, 158°33.7'W, 25 July 1967, 92-122 m. 1 male, ML 46 mm, TC-32, Stn. 29, 20°59.5'N, 158°31.5'W, 26 July 1967, 8-60 m. 1 male, ML 71 mm, TC-32, Stn. 31, 20°59.6'N, 158°29.3'W, 13 August 1967, 80-121 m, USNM 577606. 1 specimen, ML 32 mm, TC-32, Stn. 46, 20°57.6'N, 158°28.7'W, 18 August 1967, 77-118 m. 1 male, ML 50 mm, TC-32, Stn. 48, 20°59.7'N, 158°27.7'W, 19 August 1967, 60-104 m.

Description: The mantle is almost circular in cross section and is very muscular; the tail is thin and translucent. The mantle is widest at the opening (MWI 27.4-*32.3*-37.1) and the sides converge gradually toward the saccate tail. The anterior ventral margin is very slightly excavated and the lateral angles are pointed, but low. The dorsal evagination of the mantle is a rounded and low lobe.

The fins are about three-fifths of the mantle length (FLI 62.4-*64.7*-67.7) and are moderately wide (FWI 59.8-*69.3*-82.6). They arise at about the anterior third of the mantle length. The anterior margin projects as a rounded lobe near its attachment and then extends laterally, and together with the almost straight posterior margin, a rounded angle (about 72°) is formed. The posterior margins are each joined to the mantle separately leaving a small gap between them.

The funnel is triangular and almost as wide as

TABLE 5.—Measurements (in millimeters) and counts of *Enoploteuthis reticulata*. CHG = RV *Charles H. Gilbert*; HMS = RV *Hugh M. Smith*; TC = RV *Townsend Cromwell*; + = missing arm tips and lost suckers.

Cruise:	CHG-7	HMS-30	TC-32	TC-32	TC-32	TC-32	TC-7	TC-32
Station:		3	31	15	29	28	5	6
Sex	Male	Male	Male	Female	Male	?	?	?
Mantle length	130	117	71	62	46	30	26	18
Mantle width	38	32	22	23	17	12	11	10
Head width	31	30	19	17	13	12	8	8
Fin length	88	73	43	42	30	16	15	9
Fin width	85	70	48	44	38	20	18	14
Arm length								
Right I	65	58	[1]45	35	28	17	15	12
Right II	65	65	[1]46	43+	30	19	15	13
Right III	70	[1]60	[1]47	34+	30	18	16	12
Right IV	69	65	45	38	33	18	17	13
Left IV	72	66	48	40	31	19	17	13
Arm hooks/suckers								
Right I	26/—	24/8+	[1]21/24	21/20	20/15	20/11	21/14	21/14
Right II	24/—	24/19	[1]23/24	26/16	20/18	18/10	21/12	20/15
Right III	24/—	24/22+	[1]24/15	24/14	22/13	20/11	22/11	21/14
Right IV	32/—	34/17	33/20	28/11	29/9	27/12	30/9	30/10
Left IV	31/—	33/19	33/35	31/12	26/13	27/12	28/10	30/9
Tentacles right/left								
Tentacle length	120/126	93/115	76/68	80/60	47/49	22/28	20/20	—/16
Club length	20/20	21/21	16/16	—/14	14/14	8/8	6/6 5	—/5
Club hooks								
Right (dorsal/ventral)-left (dorsal/ventral)	5/5-4 5	5/6-5/6	6/6-7/5	5/5-5/5	5/6-4/5	5/5-5/5	4/5-5/5	—-3/5
Club suckers right/left								
Distal suckers	—	10/8	10/8	—	11/8	8/—	10/9	—/8+
Carpal suckers	5/4	4/6	6/6	5/5	5/5	4/6	5/7	—/6

[1]Length or count of left arm

it is long. The funnel-mantle locking cartilage is simple. The anterior end is slightly pointed and narrower than the posterior end. The groove is shallow and wider posteriorly. The funnel organ has a papilla on the anterior end of the dorsal component (inverted V-shape), is small, and has wide ridges on the lateral limbs. The ventral components are oval but have pointed anterior ends. The funnel valve is broad and its rounded anterior edge reaches the level of the funnel opening.

The head is almost square in cross section, slightly rounded at the top, and narrower than the mantle (HWI 23.8-*26.4*-28.3). The ventral excavation is moderately deep and well marked by sharp lateral edges. The three nuchal folds on each side of the head are very prominent. The first nuchal fold bears a tonguelike olfactory papilla at its posterior end. The second and third folds are crescentic folds with broad anterior ends and are united to each other posteriorly by a narrow membrane. From the posterior end of the third fold a narrow membranous ridge extends toward the dorsal midline but does not quite reach it. In large specimens the nuchal crest connects the three folds to each other and to the midline, so that three oval areas are formed on each side of the head posteriorly. The eye opening is wide and has a deep sinus. Both dorsal and ventral ocular "windows" are easy to recognize, particularly in specimens that have been preserved longer.

The buccal membrane has eight stout supports with connectives attached to the arms in the order DDVD. The lappets are pointed and the inner surface of the buccal membrane is rugose and lacks papillae. The membrane is darker than the supports; small chromatophores are present in both structures.

The arms are moderate in length; the ventral arms, which are longest, are shorter than the mantle length (ALI: I, 49.7-*56.1*-63.4; II, 50.0-*58.9*-65.2; III, 51.3-*59.1*-66.2; IV, 53.1-*61.7*-71.7). Weak keels extend along the distal third of arm I, along the distal half of arm II, and from the base to the tip of arm III. In the largest specimen the swimming keel of arm III is slightly wider than the arm width. The tentacular sheath along arm IV is narrow, about half of the arm width near the base, and reaches the tips of the arms. The protective membranes are developed on borders of all arms, but are more strongly developed on the ventral borders. This is particularly so on arm III, although the ventral membrane is never wider than the height of the hooks. The trabeculae and the membranes are very distinct even at the tips of the arms.

The right ventral arm of the male is hectocotylized (Fig. 6B). The ventral protective membrane on this arm is enlarged into an undulating lappet, which extends from near the 9th or 10th pair of hooks to the arm tip, although it becomes progressively reduced in width distally. The membrane is deeply notched at about two-thirds of its length so that two semilunar flaps of unequal lengths are formed. The dorsal protective membrane is less developed than the ventral protective membrane even in the area opposite the enlarged lappet. In addition, the males have numerous conical tubercles distributed on the oral surface, at the bases of all the arms, and on the areas between the bases of the hooks.

The arm hooks are large (Fig. 6E), arranged in two alternate rows, and enclosed by sheaths. The ventral arms of both sexes bear the most hooks. None of the hooks are unusually enlarged or reduced in either sex. The distal part of each arm has two rows of suckers. The proximal suckers in this region have long stalks and the inner rings of these suckers have seven or eight large blunt teeth (middle two teeth broadest) distally and smooth proximally (Fig. 6C). The outer ring has long pegs. The most distal pairs of suckers (with about three teeth) are much reduced in size, carried on short stalks, and have small openings.

The tentacles are generally about the length of the mantle (TLI 79.5-*100.4*-129.0). The stalk is slender, only about one-third of the width of arm III. The sides are compressed and the cross section is almost triangular. The club is narrow (Fig. 6I). The carpus includes between four and seven smooth-ringed suckers and corresponding pads arranged in an elongated series which is limited on both sides by a narrow ridge. The manus includes a dorsal row of four to seven sheathed hooks and a ventral row of five or six slightly larger hooks. The hooks (Fig. 6F) have narrow bases. The largest hooks are not bigger than any of the largest arm hooks. Marginal suckers are absent and any sucker present along the rows of hooks in young specimens certainly represents an undeveloped hook. The dactylus has 8 to 11 suckers arranged in two rows. They have long stalks and wide openings. The sucker rings bear teeth; six or seven short teeth distally and six or seven very blunt teeth proximally (Fig. 6D). The outer ring has many short pegs. The tip of the club is blunt with a short over-

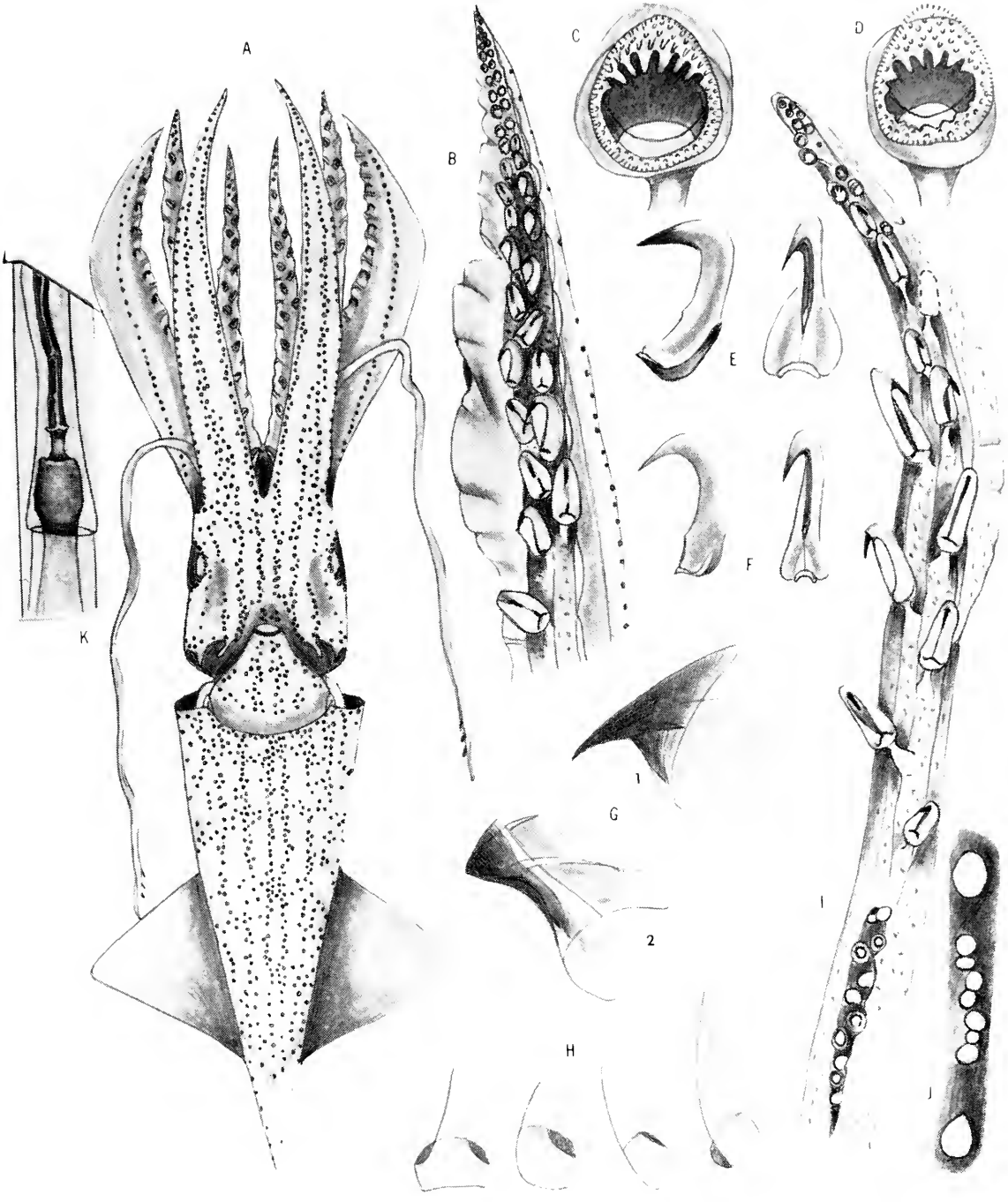


FIGURE 6.—*Enoploteuthis reticulata* Rancurel. (A, C-F, and J from female, ML (mantle length) 62 mm; other body parts are from specimens as listed.) A, Ventral aspect; B, Hectocotylus, male, ML 71 mm; C, Dorsal arm sucker; D, Tentacular sucker; E, Dorsal arm hook, oral and lateral aspects; F, Tentacular hook, oral and lateral aspects; G, Mandibles: upper (1), lower (2), male, ML 50 mm; H, Radular teeth, male, ML 50 mm; I, Tentacular club, male, ML 117 mm; J, Eye light organs; K, Section of spermatophore, male, ML 117 mm.

lapping hood which conceals a few of the suckers at the tip. The aboral keel is also narrow and extends from opposite the second hook to the lateral side of the hooded tip. Protective membranes are not developed on either side.

The photophores range in size from 0.2 to 0.4 mm. The dark or light appearance of each photophore is caused by the extent of pigmentation. The majority of the small ones are white owing to pigmentation confined only to the periphery of the photophores. The photophore pattern of the mantle is distinctive. It can be described briefly as the combined effect of about six ill-defined longitudinal rows and four oblique rows to produce a netlike or reticulated pattern (Fig. 6A). The photophores are scattered irregularly in the posterior region of the mantle, except on the tail where a single row extends on each side to the tip of the tail. The ventral area of the saccate tail lacks photophores. A single transverse row in which the photophores are farther apart dorsally lies along the anterior edge of the mantle. A few small photophores are distributed on the dorsal surface of the mantle. The fins lack photophores.

Two longitudinal rows, separated by a midline space, occur on the ventral surface of the funnel. A short row (connected to the ventral row posteriorly) is located on each side of the funnel and a long row of photophores is found on the dorsolateral side, close to each bridle.

The photophore pattern on the ventral side of the head is observed best in smaller specimens. Two clusters, separated by a narrow midline space, lie in the apex of the funnel groove. A clear space occupies the ventral midline of the head. Eight main rows of photophores (four rows on each side of the midline space) are present. The first or most medial row begins at the posterior end of the funnel groove, extends anteriorly to the ventral aboral side of arm IV, and reaches almost to the tip of this arm. The second row branches out from the first row near the apex of the funnel groove, extends parallel to the first row and joins it at a point near the base of arm IV, at about the same level as the anterior margin of the eye. At the base of arm IV the width of the second row is increased by additional photophores, and as the row continues along the base of the tentacular sheath distally it is gradually reduced to a single series of photophores which reaches the tip of the arm. A very short row or cluster of photophores occurs between the first and second rows at a short distance beyond the base of arm IV, but in older individuals this short row tends to lie closer to the second row and may be difficult to distinguish. The third lateral row extends from opposite the first nuchal fold anteriorly (interrupted by a gap at the window of the eye) to the base of arm IV where it merges with the second row. A branch continues further along the edge of the tentacular sheath almost to the tip of arm IV. The fourth or most lateral row extends from the second nuchal fold to the posterior margin of the eye and passes along the edge of the ventral eyelid to the ventral edge of the optic sinus. The row begins again on the dorsal edge of the optic sinus and continues along the base of the swimming keel of arm III to a short distance from the tip. An arclike row of small white photophores, spaced widely, lies along the ventral region of the eye between the third and fourth rows of photophores.

Nine light organs, arranged in a single row, are present on the ventral side of the eyeball. The terminal organs are much larger than the seven, closely spaced, interior light organs and are set apart from them. The interior organs are not of uniform size (Fig. 6J).

The seven radular teeth are blunt and slightly curved. The rachidian has low lateral cusps (Fig. 6H).

The mandibles are strong; the rostrum of the upper mandible is pointed and the edges are sharp (Fig. $6G_1$). The gular plate of the lower mandible is reinforced by three stout ribs (Fig. $6G_2$). At ML 45 mm the wings of both halves are already well pigmented.

The gladius is thin with a low rounded midrib. The vanes are narrow and widest at about the middle. The cone is thin-walled and as wide and rounded as the anterior end of the gladius.

The spermatophores are large. The cement gland has a large swelling at the aboral end (Fig. 6K). The aboral end of the spiral filament, anterior to the cement gland, is plain except for some longitudinal ridges. Two or three spiral turns behind the cap are present. Measurements from two specimens are given below:

	Length (mm)	
Spermatophore segment	*ML 130 mm specimen*	*ML 71 mm specimen*
Entire spermatophore	28	14
Spiral filament	12	6.2
Cement gland	3	1.8
Sperm reservoir	13	6

Young individuals: At ML 13 mm the photophores on the mantle are arranged as small clusters of large photophores distributed in a definite pattern (Fig. 2Ba). There are a few small and large photophores on the head, arms, and funnel, and they are aligned in areas that correspond to the adult pattern. At this stage there are 17 to 21 arm hooks and 7 to 11 distal arm suckers. The tentacles are shorter than the mantle (TLI 84.6) and weak. On the club a single hook, along with 16 suckers in two rows, is developed; however, the carpal area is not yet differentiated. At ML 18 mm, 20 or 21 hooks and 14 or 15 distal suckers are present on each of arms I, II, and III, and 30 hooks and 9 distal suckers are present on arm IV. On the club, 6 carpal suckers are set apart from 8 hooks (biserial) on the manus and about 13 suckers on the dactylus. At ML 26 mm the photophore pattern of the mantle appears more complex. First, additional photophores develop between the clusters whereby four oblique rows are present; and second, six longitudinal rows of indistinct small white photophores are present (Fig. 2Bb). This pattern, although not as complicated, resembles that of the adult. At this stage the clubs have 9 or 10 hooks, 9 or 10 distal suckers (biserial), and 5 to 7 carpal suckers. A ML 45 mm female has an oviducal gland 2.0 mm long, and at ML 46 mm the right ventral arm of the male is already hectocotylized, although the lappet is still very narrow and the tubercles on the arm bases are minute. There is no indication of spermatophores in the still undeveloped genital system. However, a ML 50 mm specimen has spermatophores.

Remarks: The present material can be assigned with confidence to *E. reticulata* (Rancurel 1970). The photophore patterns of the mantle, head, and arms, and characteristics of the tentacles and clubs are very close, and hook counts (arms and clubs) overlap. Differences in measurements are not considered to be significant.

Okutani (1974; 51, fig. 12a, b, e) described and illustrated a specimen, labeled n. sp. (No. 1) in his paper on the cephalopods collected at lat. 17°53′S, long. 126°18′W during the EASTROPAC Expedition, 1967-68; I have examined this particular specimen deposited in the U.S. National Museum; it is *E. reticulata*.

Enoploteuthis sp. A of Young (1978) belongs to *E. reticulata* described here (R. E. Young footnote 3).

The reticulated pattern is not unique. A similar pattern has been described for *E. galaxias* Berry, 1918. However, these two species differ in a number of basic features. Except for the mantle photophores, the pattern of the light organs in *galaxias* is unlike that of *reticulata*; there is a median row present in the head of *galaxias* flanked by three lateral rows, or a total of seven rows. A median row is absent in *reticulata*. I have examined the type of *E. galaxias* deposited at the Australian Museum, Sydney, Australia. Unfortunately, the specimen has darkened considerably and the photophore pattern is no longer recognizable with an ordinary microscope. The tentacles and clubs are very different. The tentacular stalk in *galaxias* is as stout as the arms, but in *reticulata* the stalk is only a third of the arm width. The club of *galaxias* has an expanded carpus, whereas in *reticulata* the carpus is very slender. The carpal suckers and pads in *galaxias* are arranged in a compact oval area, but in *reticulata* they are biserially arranged lengthwise in a narrow area. The suckers of the dactylus in *galaxias* are quadriserially arranged and quite numerous (38-43), whereas they are biserially arranged and very few (8-11) in *reticulata*. Lastly, the rachidian tooth of *galaxias* has no cusps, but that of *reticulata* does.

The present collection data and those from the literature show that *E. reticulata* occurs over a wide area of the Pacific, Hawaiian waters included, from lat. 28°38.5′N to 22°58′S and from long. 164°04′E to 126°18′W.

GENERAL DISCUSSION

Since the description of *Loligo leptura* by Leach (1817) and the subsequent designation of this species as the type of the genus *Enoploteuthis* Orbigny, 1848 by Pfeffer (1900), only five other valid species have been described: *E. chuni* Ishikawa 1914; *E. galaxias* Berry 1918; *E. anapsis* Roper 1964; *E. theragrae* Taki 1964; and *E. reticulata* Rancurel 1970. (See summary of history, synonymy, and generic diagnosis in Roper 1966.)

Enoploteuthis dubia Adam 1960 was described from a single specimen captured in the Gulf of Aqaba, Red Sea. However, Adam in his remarks was not certain that it was an *Enoploteuthis*. With more material and information several years later, he removed the species from *Enoploteuthis* (Adam 1973).

Enoploteuthis theragrae was described from seven specimens found in the stomach contents of two codfish, *Theragra chalcogramma*, captured in 1957 and 1962 from two localities in the Japan Sea. These specimens probably are allied to *E. chuni*. Except for the mantle photophores (six in rows for *theragrae* and eight in rows for *chuni*) all other diagnostic characters are shared by both species (M. Okiyama[4]).

GEOGRAPHIC DISTRIBUTION

Enoploteuthis anapsis and *E. leptura* are widely distributed in the Atlantic. *Enoploteuthis leptura* is known from the Gulf of Guinea (type locality), Madeira, Cape Verde Islands, the southern Straits of Florida (Roper 1966), and east of Bermuda (Roper 1977). *Enoploteuthis anapsis* is recorded from parts of the western Atlantic in the Gulf of Mexico and Caribbean Sea, from the mid-Atlantic, Madeira, St. Helena, and South Equatorial Current (Roper 1966), and east of Bermuda (Roper 1977).

Enoploteuthis chuni was first described from Toyama Bay, Sea of Japan, and Sasaki (1920) reported it later, again from Toyama Bay and farther south from Bungo Strait. Shimomura and Fukataki (1957) recorded it again from the sea of Japan together with *Watasenia scintillans* in the stomach contents of Alaskan pollock. Okutani (1967) listed an adult specimen from Sagami Bay on the Pacific side of Japan and some larval stages later (1968), also from the Pacific side of Japan. The first and only record of *E. theragrae* is from the Sea of Japan in 1964.

Enoploteuthis galaxias is known only from the type locality, off Gabo Island to Everard Grounds, Victoria, Australia.

Enoploteuthis reticulata was described from specimens taken by midwater trawl and from stomach contents of *Alepisaurus ferox* caught in areas of the southwest Pacific, approximately between lat. 22° and 18°S and long. 164°E and 133°W. The present material extends the distribution to lat. 21°N in the Hawaiian area and Okutani's specimen (1974, *Enoploteuthis* sp. No. 1) to the southeast Pacific at lat. 17°S, long. 126°W.

The genus *Enoploteuthis* was first reported from the central Pacific by King and Ikehara (1956) in their study of the food and feeding habits of the yellowfin tuna and bigeye tuna. They found a total of 36 specimens of *Enoploteuthis* in the stomach contents of these fishes. There are no other previous records of the genus from the central Pacific. The station data of the present material show that *E. obliqua* ranges approximately from lat. 11°N to 5°S and long. 81° to 144°W; *E. octolineata* from lat. 7°N to 3°S and long. 144° to 157°W; *E. jonesi* from lat. 20°N to 14°S and long. 157° to 168°W; and *E. higginsi* from lat. 21°N to 4°S and long. 149° to 169°W. Of the five species found in the central Pacific, namely, *obliqua*, *octolineata*, *jonesi*, *higginsi*, and *reticulata*, the last three species range to areas close to the Hawaiian Islands whereas *obliqua* and *octolineata* do not (Fig. 7). Based on available records, *reticulata* has the widest range; it is found in the southwest Pacific, Hawaiian area, and southeast Pacific. Collections made between September 1969 and November 1974 by the University of Hawaii include specimens of *E. reticulata* and *E. higginsi* (Young 1978).

BATHYMETRIC DISTRIBUTION

The genus *Enoploteuthis* is rare in collections, and, except for *E. anapsis* (Roper 1966), *E. higginsi*, and *E. reticulata* (Young 1978), few depth records are available.

Useful depth data are available for only two specimens of *E. leptura* studied by Roper (1966). These specimens were taken from depths between 0 and 170-300 m. *Enoploteuthis anapsis* is represented by 25 specimens taken from depths between 33 and 600 m at night and a single specimen from very deep waters, 2,000 m, during the day. Roper and Young (1975) mentioned the capture of an *E. anapsis* specimen in a closing net at 90 m, off Bermuda at night.

Depth records are not included in the original description of *E. chuni*; however, the *Albatross* specimens reported by Sasaki (1920) came from the stomach of a fish captured from deep water, about 857 m. Okutani (1967, 1968) reported an adult from a depth of 700 m and two larval stages from the surface.

The only known specimens of *E. galaxias* (four specimens) were captured at depths between 288 and 450 m.

The present material, except for that from two tows at 240 and 576 m, came from depths between the surface and 179 m. Depth data and other pertinent records are listed in Table 6 for 131 specimens of *obliqua*, *octolineata*, *jonesi*,

[4]M. Okiyama, Tokyo University, Tokyo, Japan, pers. commun. 26 November 1970.

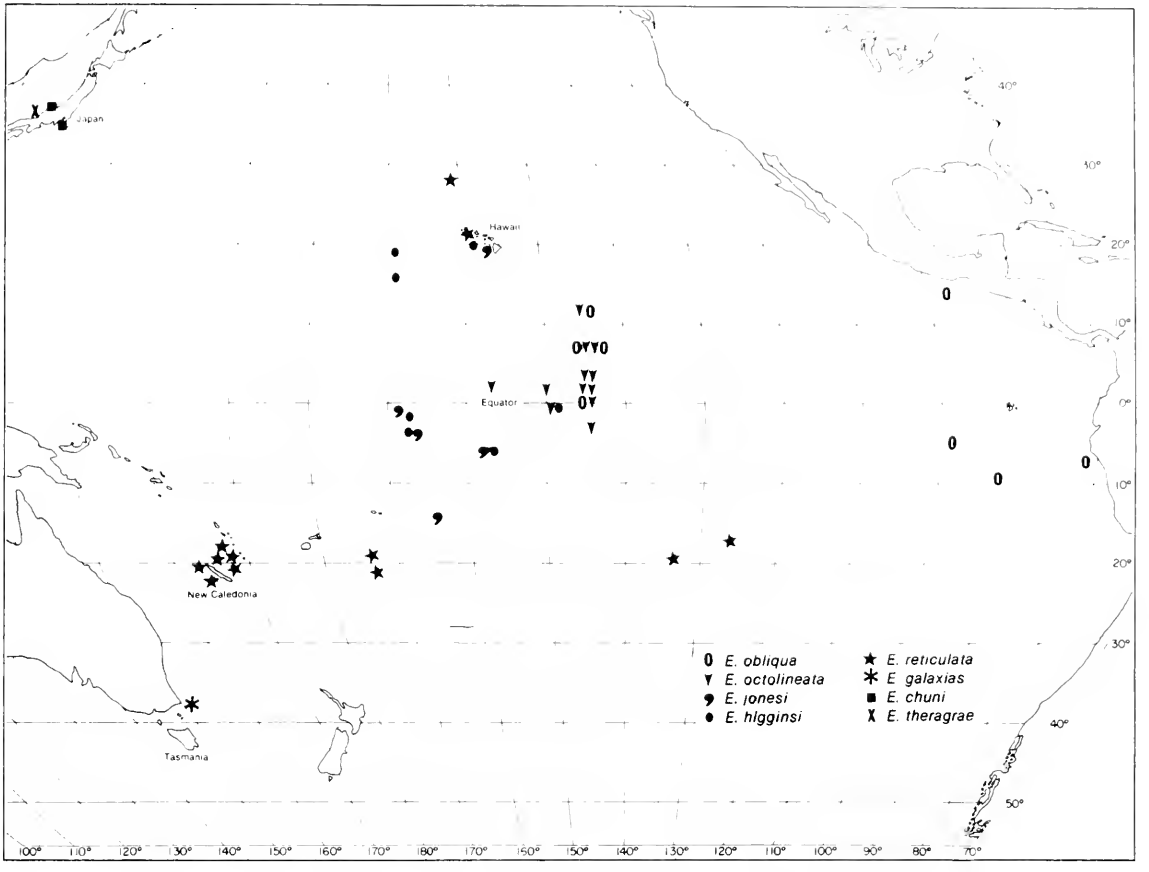


FIGURE 7.—Distribution of *Enoploteuthis* species in the Pacific.

higginsi, and *reticulata*. Most of the specimens (93.1%) were taken between the surface and 150 m, and the greatest number of these (48.1%) came from a depth of 50 m. A majority of the specimens (70.2%) were collected at night between 1900 and 0400. A limited number of specimens (8.4%) came from the few tows made during the day. *Enoploteuthis higginsi* and *E. reticulata* captured off Oahu, Hawaii, were taken close to the surface (50-100 m) at night and much deeper (500-600 m) during the day (Young 1978).

Species of *Enoploteuthis* are undoubtedly mesopelagic forms (200-1,000 m day habitat) that make diel vertical migrations as has been demonstrated for *E. anapsis* by Roper (1966) and for two other *Enoploteuthis* by Young (1978).

RELATIONSHIPS

The Pacific species of *Enoploteuthis* fall into two natural groups allied either to *E. anapsis* or *E. leptura* along the same characters that separate these two Atlantic species (see Roper 1966). Apparently, there are two species complexes within the genus: Species that tend toward the development of larger clubs and long and muscular tentacles, and those species that exhibit the opposite trends.

Additional features of the former complex are: many suckers in four rows on the clubs, large hooks, and oval to round carpal apparatus. These are features common to *galaxias*, *chuni*, *theragrae*, *anapsis*, *jonesi*, and *higginsi*. Within this group, *anapsis*, *jonesi*, and *higginsi* all have the semilunar membrane on the club while *galaxias* and *theragae* are illustrated in the literature without it. Both Berry (1918) and Taki (1964) do not mention the semilunar membrane in their species descriptions. I have seen the holotype of *galaxias*, but I could not verify the presence of the membrane because of the poor

TABLE 6.—Bathymetric data of *Enoploteuthis* species: *obliqua*, *octolineata*, *jonesi*, *higginsi*, and *reticulata*. TC = RV *Townsend Cromwell*; HMS = RV *Hugh M. Smith*; CHG = RV *Charles H. Gilbert*.

Cruise no	Station no	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
Enoploteuthis obliqua							
TC-48	19	1	58	M	50	—	April
TC-48	11	1	55	M	50	—	March
TC-46	9	1	50	F	50	1945-0230	October
TC-44		[1]1	50	F	—	—	July-August
TC-46	9	1	41	M	50	1945-0230	October
TC-48	19	1	40+	F	50	—	April
TC-44	24	1	37+	M	50	1933-0245	July
TC-44	17	[1]1	27	—	—	—	July
TC-44	24	4	12-20	—	50	1933-0245	July
TC-43	14	16	5-18	—	50	1945-0235	May
TC-43	22	5	12-17	—	50	2017-0237	May
TC-43	10	5	12-17	—	50	1943-0239	May
TC-44	18	2	12-17	—	100	1947-0253	July
TC-44	32	1	13	—	50	1937-0303	July
TC-44	54	1	12	—	50	1932-0238	July
TC-47	16	4	6-11	—	50	1930-0250	January
TC-48	16	3	7-10	—	20	—	April
TC-44	16	2	55-10	—	0	1059-0129	July
Enoploteuthis octolineata							
TC-43	52	1	75	F	50	1940-0244	May
HMS-47	58	1	71	F	212	2013-2153	November
TC-46	47	1	56	F	115	1939-0240	October
TC-46	37	1	56	F	50	1934-0236	October
TC-48	50	1	49	F	50	—	April
TC-48	52	1	46	M	50	—	April
TC-43	42	2	21-40	—	50	1942-0235	May
TC-48	35	1	39	—	50	—	April
TC-46	41	1	36	—	50	1935-0230	October
TC-48	92	1	33	—	50	—	April
TC-43	38	3	19-30	—	50	1944-0240	May
TC-44	44	[1]1	28	—	—	1935-0237	July
TC-44	26	1	26	—	20	1934-0243	July
TC-44	68	1	25	—	75	1932-0235	August
HMS-47	58	1	25	—	212	2013-2153	August
TC-43	48	1	24	—	50	1943-0240	May
TC-43	52	2	20-22	—	50	1940-0244	May
TC-43	26	1	20	—	50	1945-0235	May
TC-44	56	1	20	—	50	1933-0235	July
TC-47	45	2	16-20	—	50	2000-0200	February
TC-43	12	1	15	—	20	1945-0226	May
CHG-89	5	1	15	—	120-240	2058-2332	July
TC-46	45	2	14	—	50	1934-0234	October
HMS-47	51	1	10	—	576	2013-2158	November
Enoploteuthis jonesi							
TC-7	12	1	82	F	9-13	1926-2056	August
TC-7	12	1	47	M	9-13	1926-2056	August
TC-32	28	1	40	F	92-122	1952-0152	July
CHG-89	24	1	35	M	90-130	2053-2246	February
TC-32	46	1	35	F	77-118	1951-0151	August
TC-32	39	1	30	F	63-101	1053-0153	August
CHG-89	14	1	27	M	70-80	0258-0445	February
CHG-89	29	1	22	—	120-135	2038-2231	February
CHG-89	31	1	17	—	90-150	2040-2233	February
TC-32	37	1	11	—	55-123	0354-0954	August
Enoploteuthis higginsi							
TC-32	28	1	60+	F	8-60	1952-0152	July
TC-32	22	1	53	F	67-117	1952-0152	July
TC-32	45	1	47	F	12-31	1143-1743	August
TC-32	41	1	46	M	59-122	1151-1751	August
TC-32	23	1	46	M	17-25	0403-1003	July
TC-32	56	1	45	F	97-179	1952-0152	August
TC-32	38	2	37-40	F	8-25	1144-1744	August
TC-32	44	1	37	F	72-118	0353-0953	August
Teritu	6	1	37	M	110	—	September
TC-32	48	1	35	F	60-104	1155-1755	August
CHG-89	11	1	35	M	100-200	0254-0445	February
TC-32	37	1	32	F	55-123	0354-0954	August
TC-32	38	1	30	M	8-25	1144-1744	August
TC-32	33	1	30	F	83-99	1950-0150	August
TC-32	56	1	29	F	97-179	1952-0152	August
TC-32	46	2	27-28	—	77-118	1951-0151	August
HMS-47	51	1	27	—	576	2013-2153	November
TC-32	37	1	22	—	55-123	0354-0954	August
TC-32	33	2	12-19	—	83-99	1950-0150	August
CHG-89	29	1	16	—	120-135	2038-2231	February
CHG-51	164	1	12	—	0-100	2105-2323	February

TABLE 6.—*Continued.*

Cruise no.	Station no	No. of specimens	Mantle length (mm)	Sex	Depth (m)	Time 24 h	Month
CHG-51	172	1	12	—	0-100	2100-2250	February
CHG-89	30	1	11	—	100-125	0603-0745	February
Enoploteuthis reticulata							
CHG-7		[2]1	130	M	—	daylight	February
HMS-30	3	1	117	M	100	2105-2315	July
TC-32	31	1	71	M	30-121	0354-0954	August
TC-32	15	1	62	F	16-30	0352-0952	July
TC-32	48	1	50	M	60-104	1155-1755	August
TC-32	29	1	46	M	8-60	0343-0755	July
TC-32	9	1	45	F	17-25	0354-0954	July
TC-32	15	1	39	F	16-30	0352-0952	July
TC-32	3	1	35	F	12-15	0355-0955	July
TC-32	46	1	32	—	77-118	1951-0151	August
TC-32	28	1	30	—	92-122	1952-0152	July
TC-7	5	1	26	—	60-100	2023-2156	August
TC-32	6	1	18	—	83-124	0354-0954	July
TC-32	4	1	13	—	75-107	1146-1747	July

[1]From stomach of *Alepisaurus*.
[2]Regurgitated by a porpoise

condition of the specimen. *Enoploteuthis galaxias*, *chuni*, and *theragrae* have a midventral row of photophores on the head flanked by two lateral rows which extend (without branching) to the ventral arms. These three species are found in the western Pacific: *chuni* and *theragrae* from Japan and *galaxias* from Australia. The remaining species of this complex, *anapsis*, *jonesi*, and *higginsi*, are very similar: All have distal club sucker rings without teeth; all have an incomplete midventral row of photophores on the head (represented by a short anterior segment near the base of the ventral arms and by a triangular patch of photophores in the apex of the funnel groove); the first lateral row of photophores on the head is divided and reunited before extending to the ventral arms; and all have an incomplete photophore row on arm III. The longitudinal rows of photophores on the mantle are easily recognized in *anapsis* and *jonesi*, but not in *higginsi*.

Enoploteuthis leptura, *octolineata*, *obliqua*, and *reticulata* comprise the other species complex. They all have thin, slender, and short tentacles, clubs without semilunar membranes, few club suckers that lie in two rows, and a continuous midventral space on the head. *Enoploteuthis octolineata* and *E. leptura* are similar in that both have distinctly separated first and second lateral rows of photophores on the head, and lack a triangular patch of photophores in the apex of the funnel groove although each of the first lateral rows continues into the groove. Both species also have distinct and well-spaced mantle and funnel photophores. *Enoploteuthis reticulata* and *E. obliqua* also show similarities. The photophore pattern on the head, arms, and funnel have basically the same arrangement: Two small clusters of photophores, separated by a narrow space, are present in the apex of the funnel groove and, except for the continuous midventral space, single photophores are present posteriorly in the spaces between the funnel photophore rows. Thus, the rows are not completely separated. However, the mantle photophore pattern of each species is distinct: oblique in one and reticulate in the other. *Enoploteuthis reticulata* and *E. galaxias* have similar patterns of mantle photophores, but their head photophore patterns and some features of the clubs differ. The reticulate pattern on the mantle is probably an independently developed trait.

The spermatophores of *E. higginsi* and *E. anapsis* are both intricately sculptured, while those of *E. leptura*, *E. obliqua*, and *E. reticulata* are simple. Since the spermatophores of the other species are undescribed, it remains to be seen if the sculptured type are only associated with the first species complex and the simple type with the second complex. The important characters (except photophore pattern) of these two complexes are listed in Table 7.

KEY TO THE SPECIES OF *ENOPLOTEUTHIS* (ADULTS, WORLDWIDE)

1. Tentacular stalk and club narrow, suckers on dactylus few and in two rows; carpal cluster elongate; semilunar membrane absent 2

TABLE 7.—Some comparative features of *Enoploteuthis anapsis* and *E. leptura* complexes. ML = mantle length.

Species	Maximum ML (mm)		Tentacle length index	Club length index	Carpal suckers	Shape of carpus	Club hooks No.	Club suckers No.	Club suckers arrangement	Club sucker ring teeth No.	Semi-lunar membrane
	Female	Male									
anapsis complex											
churi	87	63	119.0-147.0	21.6-25.4	4-6	polygonal, oval	9	90	quadriserial	5-8	present
galaxias	87	73	102.6-108.3	25.6-26.4	4-6	round, oval	11	38-43	quadriserial	undescribed	absent
theragrae	80	60	83.3-91.3	25.0	5	ellipsoid	10	many, minute	quadriserial	undescribed	absent
anapsis	76.9	54	163.0-275.7	29.1-47.1	3-4	rectangular	12-13	40-50	quadriserial	absent	present
jonesi	82	47	104.9-188.9	24.4-40.7	3-4	round	13-14	60-72	quadriserial	absent	present
higginsi	60+	46	110.8-239.1	29.7-36.1	2-3	oval	10-12	60-72	quadriserial	absent	present
leptura complex											
leptura	44.5	79	89.0-96.0	17.9-20.6	5-6	elongate	6-12	10-15	biserial	7	absent
obliqua	50	58	62.1-96.4	17.0-26.0	4-5	elongate	8-9	11-17	biserial	6-7	absent
reticulata	62	130	79.5-129.0	15.4-30.4	4-7	elongate	8-12	8-11	biserial	6-7	absent
octolineata	75	46	93.3-112.7	25.0-28.3	3-6	elongate	9-11	16-17	biserial	10	absent

1. Tentacular stalk and club robust, suckers on dactylus many and in four rows; carpal cluster round to oval; semilunar membrane present or absent 5

2. Mantle photophores in longitudinal rows only 3
2. Mantle photophores in longitudinal and/or oblique rows 4

3. Eight well-spaced mantle rows, all reaching anterior mantle edge; eight photophore rows on head, second and third lateral rows united posteriorly ..... *octolineata*
3. Seven well-spaced mantle photophore rows, only six reaching anterior mantle edge; eight photophore rows on head, none united ..... *leptura*

4. Two photophore rows on median part of mantle, oblique photophore rows on sides ..... *obliqua*
4. Longitudinal rows and intersecting oblique rows of photophores on mantle (reticulate pattern) ..... *reticulata*

5. Midventral photophore rows on head complete; first and second lateral photophore rows unbranched; photophore row on arm III complete 6
5. Midventral photophore row on head incomplete; first lateral photophore row on head divided and reunited; photophore row on arm III incomplete 8

6. Eight photophore rows on mantle, distinct for one-third of mantle length; semilunar club membrane present ..... *churi*
6. Six photophore rows on mantle or no rows, photophores scattered; semilunar club membrane absent 7

7. Six photophore rows on mantle, photophores scattered on posterior half of mantle ..... *theragrae*
7. No photophore rows on mantle, mantle photophores scattered; some areas devoid of photophores ..... *galaxias*

8. Mantle photophores not in rows, photophores scattered ..... *higginsi*
8. Six longitudinal photophore rows separated by narrow space 9

9. Midventral space not extending to tail, this space occupied by scattered photophores near tail ..... *anapsis*
9. Midventral mantle space narrow, extending to tail ..... *jonesi*

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LIFE HISTORY STUDIES OF THE SANDWORM, *NEREIS VIRENS* SARS, IN THE SHEEPSCOT ESTUARY, MAINE

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ABSTRACT

Little information is available on the life history of the sandworm, *Nereis virens*, in Maine despite their commercial importance over more than 40 years. Life history studies were performed in a flat along the Sheepscot River at Wiscasset, Maine, which was closed to commercial digging. Salinity varied between 17 and 29‰ at the surface and between 24 and 29‰ on the bottom, and temperature varied between −1° and 15°C at the surface and −1° and 14°C on the bottom. The proportions of potential male and female spawners changed with size; for worms <30 cm, the proportions were equal whereas a preponderance of females existed for worms >30 cm. Thirty percent of the largest worms displayed no sign of sexual development. Single eggs of 50 μ diameter were first observed in the coelom from October to November. These eggs entered a rapid growth phase between August and December and attained a maximum diameter of from 183 μ (1967) to 194 μ (1968) at time of spawning during April and May. Maturation could take as long as 18-20 months or as little as 12 months. The numbers of eggs laid by sandworms were found to vary between 0.05 (16 cm worm) and 1.3 million eggs (54 cm worm). The onset of spawning occurred when the surface water temperature was between 7.0°C (1968) and 8.1°C (1967) and when the bottom water temperature was between 6.7°C (1968) and 7.6°C (1967). During both years, spawning occurred 4 days after full moon during the period of spring tides. Scuba observations revealed that male spawners emerged from the mud about 3 hours after high water. At the peak of spawning, densities of epitokes may reach 1 worm/m^2. Male spawners are readily consumed by herring gulls, *Larus argentatus*.

The sandworm, *Nereis virens* Sars, commonly occurs on the Atlantic coast from Virginia northward to the Arctic region. It is also found in Iceland, Norway, Ireland, and the North Sea to France (Pettibone 1963).

Nereis virens is known to inhabit coarse and fine muddy sand, mussel beds, and the roots of decaying marsh and eelgrass (Pettibone 1963). The sandworm population in the Sheepscot River study area at Wiscasset, Maine (lat. 44°N, long. 70°40′W), inhabits a gray, silty clay which is moderately burrowed and contains shell fragments, mica flakes, and 2% organic carbon (Reynolds et al. 1975[2]). The mean tidal amplitude in this region is 2.9 m.

Ecologically, sandworms occupy an important position in the food web of other invertebrates, fish, and shorebirds. They have been harvested commercially for bait along the Maine coast for more than 40 years, with landings of 26.9-38.1 million worms/yr and a landed value of $0.5-1.1 million reported between 1966 and 1980 (NMFS 1966-80).

Previous research on Maine sandworms included studies on digging (Ganaros 1951[3]) and dispersion (Gustafson 1953; Dean 1978). Although intensive harvesting qualifies the sandworm for management considerations, only reports by Glidden (1951)[4] and Dow and Creaser (1970) contain life history information pertinent to management of sandworm populations in Maine. The present study was undertaken to provide life history information for a sandworm population in the Sheepscot Estuary at Wiscasset, Maine. It also includes some information on subjects not previously investigated or which differ from findings reported from other geographical locations.

Other studies on the life history and reproduction of *Nereis virens* include Brafield and Chapman (1967) and Bass and Brafield (1972) in the Thames Estuary at Southend, England; Sveshnikov (1955) in Rugozerski Bay near the White Sea,

[1]Maine Department of Marine Resources Research Laboratory, West Boothbay Harbor, ME 04575.

[2]Reynolds, L., J. Bowman, and E. Kelly. 1975. Unpublished summary of sediment size, x-radiography, chemistry, and mass physical properties of six cores and two grabs from Maine. U.S. Naval Oceanographic Office, Washington, D.C.

[3]Ganaros, A. 1951. Commercial worm digging. Bull. Dep. Sea Shore Fish., Augusta, Maine, 6 p.

[4]Glidden, P. E. 1951. Three commercially important polychaete marine worms from Maine. Rep. Dep. Sea Shore Fish., Augusta, Maine, 25 p.

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Russia; and Snow and Marsden (1974) at Brandy Cove, St. Andrews, New Brunswick, Canada.

Materials and Methods

All sandworms were collected in the vicinity of a small intertidal mud flat at Wiscasset, Maine, closed to commercial digging. Within this area, a section running parallel to the low-water mark and measuring 91 m × 24 m was used for experimental purposes. Differences in tidal height between the upper and lower extremities of this experimental area were about 22 cm. Monthly, three 1 m^2 sample plots were randomly chosen and dug within the experimental site. The sampling device consisted of a 1 m^2 frame with deep walls (45 cm) that could be pushed into the mud to prevent escape. Within each plot, the surface ooze was removed with a dustpan to a depth of 2-3 cm and deposited within a square framed receptacle constructed of 1 mm mesh fiberglass screen. The receptacle was then partially immersed in the river and carefully agitated to remove sediment. The remaining debris and worms were poured into a plastic container and transported to the laboratory. Small portions of debris, together with seawater, were deposited in dissecting trays and dispersed with a needle probe. The contents were thoroughly searched and all small sandworms, swimming or hiding among the debris, were removed with forceps. Clumps of deeper and firmer mud were removed from the sampling device in the field to the maximum depth of burrowing activity (about 30 cm) and carefully broken by hand to remove the larger worms intact. These worms were also transported to the laboratory in plastic buckets.

All sandworms were acclimated to high salinity water (about 32‰) at the laboratory prior to immersion in anesthetic (7.5% $MgCl_2$). Lengths were obtained using a V-shaped measuring trough containing ample anesthetic to cover the worms. Coelomic fluid was withdrawn with the aid of capillary pipettes, and sex was determined by microscopic examination of the contents. Egg diameters were measured with an ocular micrometer and without a cover slip. Usually 10 eggs were measured from each worm. The relationship of sandworm length to numbers of eggs laid was corrected for transformation bias following the methodology of Bradu and Mundlak (1970).

Worms used in the study to determine the percent of mature males and females and immature females in each length increment were obtained during February (prior to spawning) from pooled samples dug independently of the regular monthly sample. The distinction between mature and immature females was made after examining eggs in the coelomic fluid; large eggs from mature worms would be spawned in April or May, and small eggs would be spawned approximately 1 yr later. We were unable to make a distinction between mature and immature males.

Sandworms designated "nonspawners" include worms of all sizes that have not spawned and whose coelomic contents present no clue about sexuality. "Spent" worms include both males and females that have spawned and are deteriorating and approaching death.

Female sandworms used for egg counts were anesthetized, measured, and preserved. The worms were then split lengthwise and washed thoroughly to remove as many eggs as possible. Next, the body was chopped into 1 cm pieces, immersed in seawater, and stirred magnetically. After three or four changes of water, most eggs were dislodged. Egg samples were diluted in 0.1-2.7 l seawater, depending upon size of the worm and numbers of eggs present. Two 1 ml aliquots were withdrawn from this mixture during agitation, placed on Sedgwick-Rafter[5] counting cells, and the number of eggs counted under the 10× objective. The mean value was then multi-

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

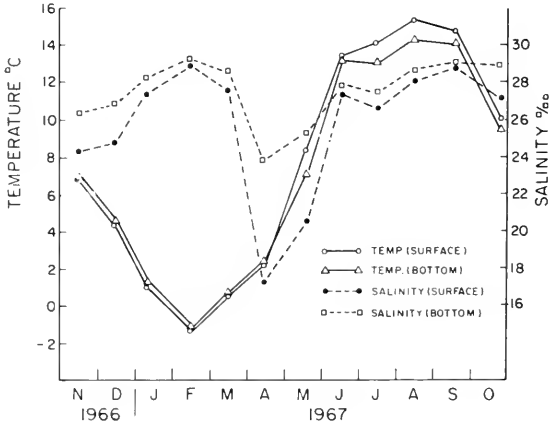

FIGURE 1.—Summary of temperature and salinity data collected from the Sheepscot River near the Wiscasset closed area between November 1966 and October 1967.

plied by the dilution factor to obtain the final egg count.

Hydrographic data were usually obtained shortly after the collection of worm samples. Mean monthly water temperature was calculated from 25 thermister recordings collected in situ at 30-min intervals at hydrographic stations occupied for 12 h. Mud temperature records were collected in situ by digging a shallow hole in the mud flat and inserting a thermometer horizontally at a depth of about 10 cm. Water samples used in salinity analysis were obtained using a 1 l water sampler. Water samples of 5 ml were analyzed for salinity by the Knudsen method.

Sandworms were captured during spawning using scuba techniques or dip nets.

RESULTS

Salinity and Temperature of the Study Area

The salinity and temperature regime of the river water at the study area during the period November 1966-October 1967 is summarized in Figure 1. During these studies, surface salinity varied between 17 and 29‰, surface temperature between −1° and 15°C, bottom salinity between 24 and 29‰, and bottom temperature between −1° and 14°C.

Length Frequency

Preliminary digging in the Wiscasset closed area indicated that sandworms were most abundant in the region of the low-water mark. Within this region, significant variations in both abundance and size were recorded for three randomly selected 1 m^2 plots dug from one tidal height during one time period. Because of this variation, digging more than 1 sample plot/mo was desirable. We elected to dig and combine the results of 3 randomly selected plots/mo because the combined results produced fairly consistent length-frequency trends between months. Considerable breakage of all sizes of sandworms was encountered during handling and processing. During agitation, the presence of sharp shells and debris in the upper layer of organic ooze resulted in additional breakage of juvenile sandworms prevalent there. Some unavoidable bias has therefore resulted in the numbers of juvenile worms reported. Length-frequency results for all whole worms collected during August, September, and October are shown in Figure 2. Sandworms captured varied in length between <1 and 31 cm. Numbers of whole individuals captured during these months varied between 546 and 701. Figure 2 indicates some recruitment of small individuals into the sampled population during the summer. Additional length-frequency information collected during this study is presented in Creaser and Clifford (1981)[6].

The August-October 1967 length-frequency data, when combined to produce sufficient number, was analyzed by the method of Harding (1949), as explained by Cassie (1950), to determine the number of assumed age modes. Although five assumed modes and linear growth were detected by this analysis, there is considerable overlap in length at age; the results are therefore questionable until they can be verified against other aging techniques.

[6]Creaser, E. P., and D. A. Clifford. 1981. Life history studies of the sandworm *Nereis virens* Sars, in the Sheepscot Estuary, Maine. Maine Department Marine Resources Research Laboratory, Res. Ref. Doc. 81/16, 37 p.

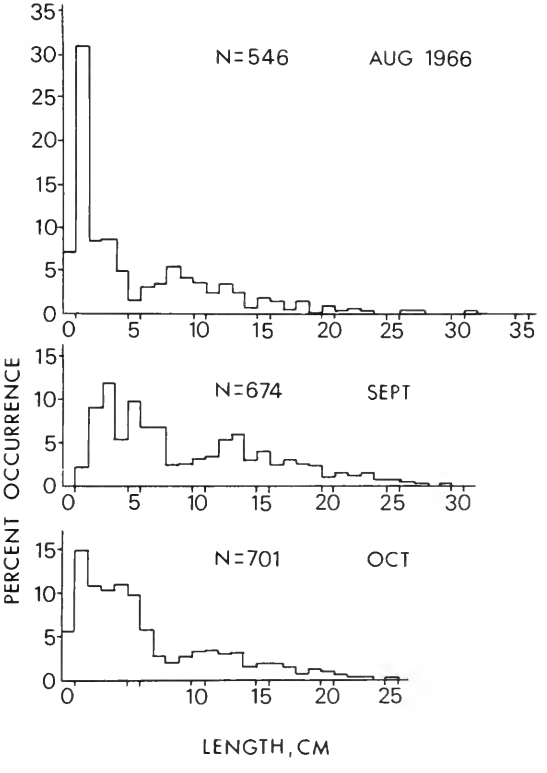

FIGURE 2.—Monthly length frequency distributions for three combined plots dug from the Wiscasset closed area.

Proportions of male, female, and nonspawning sandworms of various lengths are shown in Figure 3. There is an increase in numbers of mature males and females with increasing size. Worms >30 cm show a preponderance of mature females over mature males. More than 30% of the largest worms showed no sign of sexual development.

Oocyte Development

The results of oocyte growth studies are presented in Figure 4A, and water temperatures associated with these data are shown in Figure 4B. Eggs of about 50 μ were first observed in the coelom in October-November. Diameter increased from 80 to 160 μ during the rapid-growth phase which occurred between August and December. Prior to spawning, the rate of egg growth decreased. Maximum mean egg diameters obtained were 183 μ (1967) and 194 μ (1968). A Student's t-test revealed a significant difference between these mean diameters ($t = 4.65910$; $P<0.05$; 14 df). Spawning occurred in April and May during a 4-5 wk period, and few egg-bearing worms were found after the beginning of June. The maturation of gametes required 18-20 mo, or as little as 12 mo, depending upon when the eggs were ovulated into the coelom. Annual spawning, together with a maximum development period of 18-20 mo, accounted for the presence of two general egg sizes in sandworms inspected between October-November and April-May. Eggs approaching spawning size varied the least in diameter (the smallest standard deviation) (see Figure 4A). During the period of rapid egg growth, both mud and bottom river temperatures were decreasing (see Figure 4B).

Numbers of Eggs Laid

The numbers of eggs laid by sandworms of various lengths are recorded in Figure 5. The range varies between about 0.05 and 1.3 million eggs for worm lengths of 16 and 54 cm, respectively.

Environmental Conditions During Spawning

Spawning first occurred in the Wiscasset region on 28 April 1967 and 17 April 1968. A summary of hydrographic conditions associated with spawning on 2 May 1967 and 19 April 1968 is presented in Table 1. Table 1 shows that mean surface-water temperatures of 7.0°C (1968) and 8.1°C (1967) and bottom water temperatures of 6.7°C (1968) and 7.6°C (1967) were associated with the onset of spawning. During both years, initial activity in the Wiscasset area occurred 4 d after full moon during the period of spring tides. The stage of the tide during which spawning activity occurs was investigated on 23 April 1968, using scuba techniques. During a series of six dives beginning just after high water (08:28

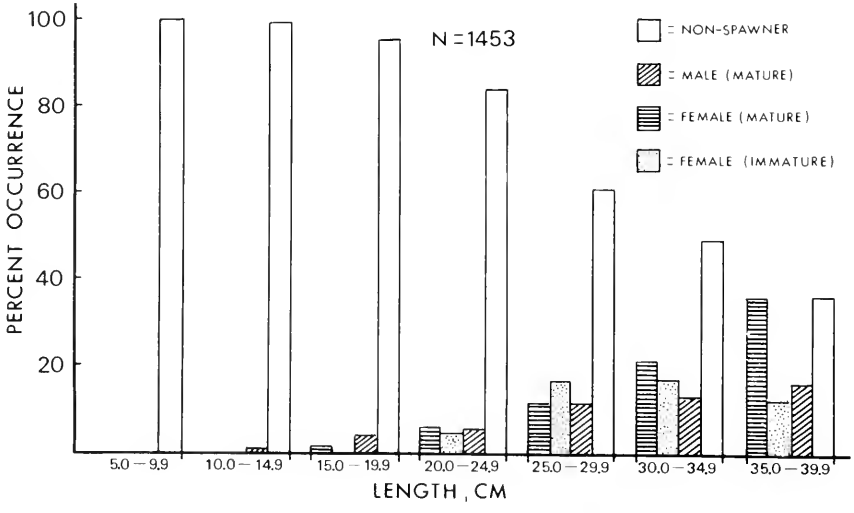

FIGURE 3.—Proportions of male, female, and nonspawning sandworms of various lengths collected prior to spawning during February 1967.

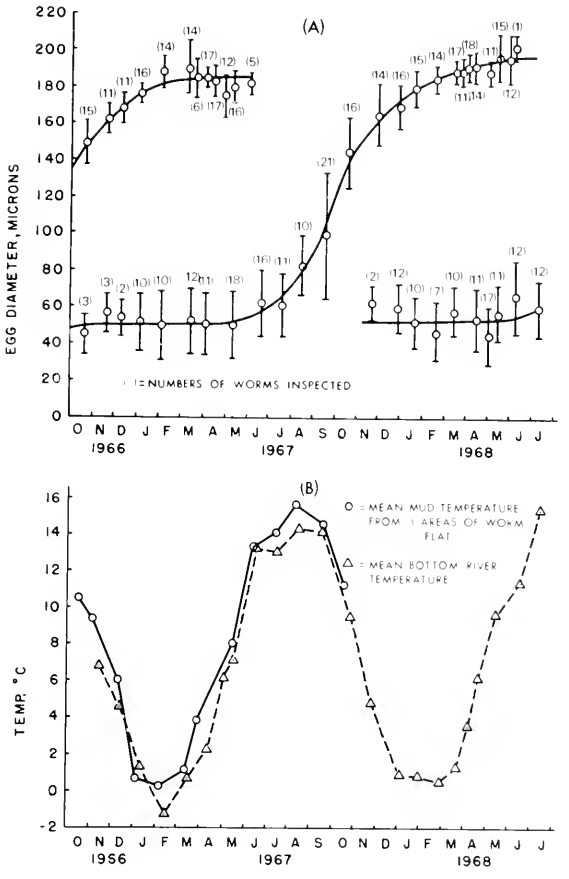

FIGURE 4.—(A) Oocyte growth occurring simultaneously in two groups of Wiscasset sandworms at different stages of maturation (lines fitted by eye). (B) Monthly mean mud and bottom water temperature from the Sheepscot River at Wiscasset.

TABLE 1.—Summary of temperature and salinity associated with sandworms spawning at Wiscasset, Maine, on 2 May 1967 and 19 April 1968.

	2 May 1967 1030-1430 h			19 April 1968 0730-1200 h		
	Temp. (°C)	Salinity (‰)	N	Temp. (°C)	Salinity (‰)	N
Surface						
$\bar{x} \pm 1$ SE	8.1±0.3	19.98± 0.38	9	7.0±0.2	23.55± 0.25	10
Range	6.8–9.1	18.51–21.58	9	5.8–7.8	22.75–25.08	10
Bottom						
$\bar{x} \pm 1$ SE	7.6±0.2	23.18± 0.43	9	6.7±0.2	25.34± 0.26	10
Range	6.6–8.4	21.24–25.32	9	5.3–8.0	23.80–26.09	10

EST) and ending just before low water (14:34 EST), no spawning worms were observed until about 3 h after high water (Table 2). Although the possible role of water temperature in initiating spawning cannot be completely eliminated,

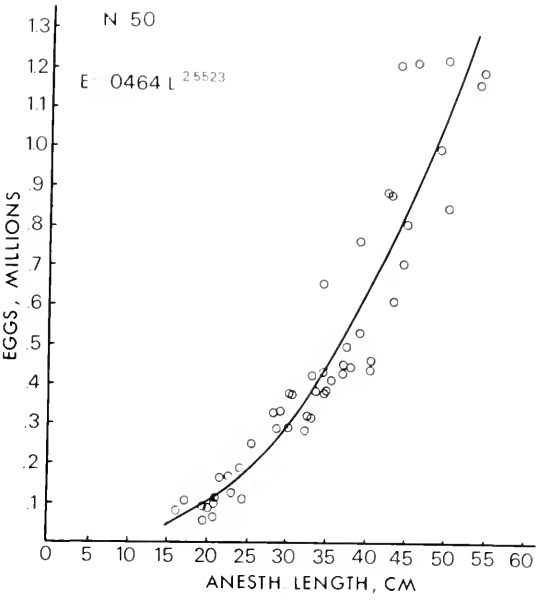

FIGURE 5.—Number of eggs produced as a function of sandworm length.

the tidal-condition results in Table 2 are consistent with numerous visual observations on spawning activity in the Wiscasset area over many years.

Spawning Characteristics

Nearly all sandworms captured during spawning were males. Females were only rarely encountered in the latter part of the spawning season. Scuba observations revealed that male sandworms emerge from the mud anterior-end

TABLE 2.—Data collected during scuba investigation of tidal conditions between high water and low water at onset of spawning activity on 23 April 1968.

Time of dive	Tide height (m)	Temperature (°C)		Salinity (‰)		No. worms collected	
		Surface	Bottom	Surface	Bottom	♂	♀
(High water 0828 h EST)							
0910-0930	3.4	7.3	6.1	24.24	26.64	0	0
1010-1028	2.9	7.6	6.5	25.12	26.24	0	0
1103-1123	2.1	8.1	7.7	24.87	24.74	0	0
1200-1222	1.2	8.8	8.2	24.61	24.69	127	0
1305-1335	0.6	9.4	9.1	25.16	25.26	118	0
1400-1410	0.5	11.2	10.4	24.72	24.98	96	0
(Low water 1434 h EST)							

first. These free-swimming spawners displayed two characteristic types of swimming behavior: 1) Swimming more or less in a straight path (with occasional tumbling and back swimming) with typical lateral undulations of the body, and 2) swimming in circles typically 10-15 cm in diameter. Spawning worms appeared to be distributed randomly over the flats. During peak spawning, the density of worms observed swimming near the surface of the mud was about 1 worm/m^2. All male spawners collected in the Wiscasset area were definitely epitokous individuals, having undergone morphological changes. Mature female sandworms dug from the flats were typically dark green, males that had just emerged to spawn were lighter green, and males that were "spawned out" but still swimming were a dark, bluish green. Some male sandworms may spawn during more than one tide. Numerous male sandworms were observed burrowing back into the flats during scuba dives. None, however, burrowed deeply into the mud. The reproductive strategy of the sandworm qualifies it as a "monotelic" species, i.e., it breeds once in its lifetime, all gametes are released in one or two large batches, and the spent animals die immediately or shortly afterwards without developing more gametes (Clark cited in Stancyk 1979). Some nearly "spent" individuals were observed to contain large numbers of a parameciumlike ciliate.

Predation

During receding tides in the Wiscasset vicinity during April, an increasing number of herring gulls, *Larus argentatus* Pontoppidan, circling the flats, anticipated the ensuing spawning activity of *Nereis virens*. At the height of spawning, thousands of gulls could be observed feeding on male spawners.

DISCUSSION AND CONCLUSIONS

Salinity and Temperature of the Sandworm Habitat

The salinity and temperature regime encountered by *Nereis virens* in other geographical areas is incomplete. Brafield (1968)[7] indicated that water and interstitial salinity encountered by the Southend, England, sandworm population varied between 28-32‰ and 27.5-31.5‰, and water temperature varied between 3.2°C (January) and 22.5°C (August). The Wiscasset population is subjected to more estuarine salinity conditions and cooler water temperatures than in England. The temperatures recorded for Brandy Cove, New Brunswick, by Snow (1972) are very similar to the temperatures recorded in Figures 1 and 4B.

Length-Related Observations

The concave nature of the length-frequency data presented in Figure 2 is consistent with a highly variable recruitment pattern resulting from larval mortality and intense predation soon after settlement (Warwick cited in Coull 1979).

The absence of sexual products in the coelom of a proportion of the largest sandworms (see Fig. 3) appears to be characteristic of the species. Both Snow and Marsden (1974) and Brafield and Chapman (1967) have made similar observations. The fate of these large nonspawners is not known. They possibly emigrate to subtidal or downriver habitats or succumb to natural or digging mortality without spawning.

Considerable variation exists in the maximum size of *Nereis virens* reported from different geographical locations. The largest individual reported in Figure 2 was 31 cm. Sandworms of 70-75 cm (anesthetized length) have been dug from the Back River in Boothbay, Maine (lat. 43°54′15″ N, long. 69°40′ W). Sveshnikov (1965) reported catching epitokous individuals 45 cm in length and also reported that the heteronereid form of *N. virens* reached a length of 90 cm along the coast of England and 1 m in Japan. Khlebovich (1963) reported mature individuals reaching 38.5 cm in the White Sea.

The sex ratio of *Nereis virens* collected prior to spawning varies with geographical location. In our studies, the sex ratio of small potential spawners was approximately 1 female:1 male, whereas the sex ratio of individuals ≥30 cm was approximately 2 females:1 male. There is no reason to believe that these changes in sex ratios with size result from nonspawners (in February) becoming sexually mature by spawning onset in April. Our observations reveal that the maturation rate of both eggs (see Figure 4A) and sperm requires considerably more than 2 mo. The change in sex ratio may indicate that larger potential males are more disposed to either free-swimming in the

[7]A. E. Brafield, Department of Biology, Queen Elizabeth College (University of London), Campden Hill Road, London, England, pers. commun. 1968.

water or exposing themselves on the surface of the mud, and are therefore subject to greater natural mortality through predation. The free-swimming habits of *Nereis virens* (especially at night) have been well documented (Crowder 1923; Gustafson 1953; Dean 1978). Brafield and Chapman (1967) reported that by the onset of spawning, males and females occurred in about equal numbers. Snow (1972), on the other hand, reports a 3:1 ratio of males to females prior to spawning.

Oocyte Development

Some similarities exist between our studies of oocyte development (see Figure 4A) and those of Brafield and Chapman (1967) and Snow and Marsden (1974). Brafield and Chapman (1967) reported that ovulation occurred in February or March at 50 μ and the oocyte diameters increased from 80 μ to 160 μ during the period of rapid growth between September and December. The increase in oocyte diameters to 170-180 μ prior to spawning required about 14 mo. Snow (1972) reported that the smallest eggs found free in the coelom of *Nereis virens* measured 10 μ in diameter. The eggs usually remained in clumps until they measured 25 μ and appeared singly above 50 μ. Snow and Marsden (1974) stated that the rapid-growth phase began in September, and their egg growth figure showed that this extended at least until December. They stated that maturation required 1-2 yr, depending upon the time of year when the eggs were produced. Ova measured 210-240 μ when spawned in May.

The standard deviation for oocyte diameters recorded in both the present study and that of Brafield and Chapman (1967) reveals that small oocytes are more variable in size than large oocytes. The large standard deviation for small oocytes results from ovulation occurring over a long period. Eventually, the maturation rate of oocytes produced late in this period accelerates so that all oocytes mature at a certain size at the same time (Clark cited in Stancyk 1979). Similar observations have been recorded for *Nereis diversicolor* Müller (Clark and Ruston 1963).

Oocyte development in *Nereis virens* follows the typical sigmoid growth curve. Similar observations have been recorded for all or part of the oocyte maturation processes in *Arenicola marina* Linnaeus (Howie 1964 pers. commun. cited in Clark 1965), *Nereis diversicolor* (Clark and Ruston 1963), and *Glycera dibranchiata* Ehlers (Creaser 1973).

Although no length measurements were obtained for the sandworms used in Figure 4A, it was generally evident to us that no relationship existed between size of the adult and size of the eggs; potential spawners of all sizes at one time possessed eggs of similar size.

Numbers of Eggs Laid

Sandworms >37 cm long were not found in the Wiscasset closed area (Creaser and Clifford footnote 6). However, a few larger worms, up to 54 cm long, were captured adjacent to the closed area after extensive digging, and egg counts from these as well as the more typical sizes were included in this study. Sandworms contained considerably fewer eggs than were found in similar-sized bloodworms, *Glycera dibranchiata*, collected from the same closed area but higher on the flat (Creaser 1973). The relatively large numbers of eggs produced (0.05-1.3 million), however, are consistent with the observation that macrofauna species generally produce large numbers of gametes (Thorson 1950 cited in Coull 1979).

Environmental Conditions During Spawning

Clark and Olive (1973) reported that "In the family Nereidae, sexual maturation and epitoky are caused by a decline in the rate of production of a cerebral hormone." Clark (1965) suggested that changes in the secretion rate of cerebral hormone might be controlled by environmental conditions or by some feedback mechanism. A distinction is made between (a) necessary environmental conditions and (b) specific environmental signals (Clark cited in Stancyk 1979).

Results of the present study suggest that a water temperature of about 7°-8°C might be one of the necessary environmental conditions required to initiate spawning. This hypothesis is strengthened by the fact that Snow and Marsden (1974) successfully fertilized *Nereis virens* ova and reared the young in the laboratory at 7°C. Sveshnikov (1955) recorded that surface temperature varied between 8.9° and 9.5°C at time of spawning in the White Sea. Some investigators (Thorson 1946; Korringa 1957) have reported that a rise in seawater temperature triggers spawning in a number of marine organisms. Bass and Brafield (1972) induced premature spawn-

ing in *Nereis virens* with an artificial rise in temperature from ambient (5°C) to 22°C over a 10-h period.

The specific environmental signals required to initiate spawning may be associated with the phase of the moon and the stage of tide. Our observations of initial spawning activity shortly after full moon are in partial agreement with Pettibone (1963) who reported that the spawning activity of *Nereis virens* on the New England coast centered around both full and new moon. Brafield and Chapman (1967), Bass and Brafield (1972), and Snow and Marsden (1974) have reported that swarming coincided with the time of new moon. The sandworms at Wiscasset spawn during the second half of the outgoing tide through the first part of the incoming tide. Pettibone (1963) reported similar observations from Barnstable, Mass. Bass and Brafield (1972) reported swarming in the Thames population only during periods of day and night high tides. Our only observation of some exceptionally large *Nereis virens* swarming at high water occurred in the Damariscotta River, Maine, in the vicinity of Fort Island (lat. 43°53′30″ N, long. 69°31′30″ W).

Spawning Characteristics

Some of the characteristics of spawning *Nereis virens* recorded by different investigators are summarized in Table 3.

Nereis virens has been described as atokous (Brafield and Chapman 1967; Snow and Marsden 1974) and epitokous (Gustafson 1953; Sveshnikov 1955; Khlebovich 1963). Clark (1961) reported that the structural modification associated with epitoky may be subtle and consist only of an elongation of the setae, modification of the sense organs, and reconstruction of the musculature. According to this description, spawning individuals captured in the vicinity of Wiscasset were obviously epitokes; the same morphological changes recorded in England by Bass and Brafield (1972) for adult males were observed in the Wiscasset population. There is no reason to doubt that *Nereis virens* display different reproductive characteristics in different geographical locations. Dales (1950) reported that nereids are well known for displaying variable reproductive habits within a given species.

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TABLE 3.—Some characteristics of spawning *Nereis virens* recorded by different investigators.

Investigators	Location of spawning males	Location of spawning females	Male swimming behavior during spawning	Color of spawners	Fate after spawning
Bass and Brafield (1972)	males in free-swimming swarms	believed females spawned in burrows	observed circular swimming in both vertical and horizontal plane; anterior portion of gravid worm becomes rigid.	4% of males deep red with white lines marking margin of anterior segments, a few were creamy white	worms swarmed several times before becoming spent but die after spawning
Brafield and Chapman (1967)	males in free-swimming swarms	believed females spawned in burrows or possibly spent short period swarming at surface		females lime green males milky green	worms die after spawning
Clark (1961)	males often dominate breeding swarms of nereids		swimming in tight circles is common to all swarming nereids		
Snow and Marsden (1974)	males in free-swimming swarms	believed females spawned in burrows			survival after spawning is highly unlikely
Our observations	males in free-swimming swarms	believed females spawned in burrows; some evidence that they emerge from mud to die after spawning	2 types: 1) swimming in straight lines is characteristic of new spawners that have just emerged from the mud, 2) circular swimming of spent or nearly spent individuals caused by anterior portion curved downward and worm tipped on side when swimming	females dark green males pale green becoming darker as worms become spawned out	individual worms sometimes spawn on more than one tide but die after spawning

photographic services, and Vicki Averill for typing.

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DIET OVERLAP BETWEEN ATLANTIC COD, *GADUS MORHUA*, SILVER HAKE, *MERLUCCIUS BILINEARIS*, AND FIFTEEN OTHER NORTHWEST ATLANTIC FINFISH

RICHARD W. LANGTON[1]

ABSTRACT

Diet overlap calculated as the percentage similarity between the diets of Atlantic cod, *Gadus morhua*, silver hake, *Merluccius bilinearis*, and 15 other finfish species was computed from stomach contents data collected in the northwest Atlantic between Cape Hatteras, North Carolina, U.S.A., and western Nova Scotia, Canada, from 1973 through 1976. Since crustaceans are preyed on by both Atlantic cod and silver hake and most of the 15 other groundfish species representing members of the Rajiformes, Perciformes, Gadiformes, and Pleuronectiformes, completely dissimilar diets occur very rarely. Although the overlap values are quite variable, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and species from the three other ordinal taxonomic levels. Furthermore, Atlantic cod and silver hake show a size dependent shift in diet (at 60-70 cm for Atlantic cod and 20-25 cm for silver hake) from crustaceans to fish so that, generally, the major overlap levels are for the smaller size classes of fish. Overlap levels are discussed in relation to the prey species the predators share and also in terms of their usefulness in identifying potential trophic linkages between northwest Atlantic finfish.

The traditional way of identifying fish is by recognizing individual species as discrete taxonomic units. Although the species concept is fundamental to any biological work, fishery biologists have been considering other means of grouping species. These are usually attempts to lump species in an ecological sense and they often depend on the fishes' diet. These feeding niche groupings may then be related to the morphology and size of the fish or the prey. Food related size classes for fish have, for example, been identified by Parker and Larkin (1959), Paloheimo and Dickie (1965), and Tyler (1972). These classes are referred to as threshold lengths or feeding stanzas. Grouping of fish based on gut morphology alone has been explored extensively for flatfish by deGroot (1971), while prey size grouping was developed by Ursin (1973) and applied to northwest Atlantic fish by Hahm and Langton (1980[2]). More recently, scientists on the west coast of the United States have been looking at Pacific fish assemblages (Gabriel and Tyler 1980) and have proposed the idea of an Assemblage Production Unit (Tyler et al. in press). The Assemblage Production Unit is defined as a geographically limited natural production system of interacting organisms, in which all production is trophically linked.

The key to all these schemes of species independent linkages is a complete understanding of whatever criteria are used to group like animals. In the present paper, fish predators have been grouped by species in 5 cm size classes and the diet of each 5 cm length group described quantitatively as a percentage weight of the total stomach contents for each group. Diet overlap has then been calculated for each species-size class combination and the overlap levels related to actual diet composition. Although diet overlap calculations have their limits (discussed in Langton and Bowman 1980), as do any other methods of data reduction, this paper offers one way of evaluating real and/or potential trophic linkages between northwest Atlantic finfish.

METHODS

Stomachs were collected from both demersal and pelagic fish by personnel at the Northeast Fisheries Center Woods Hole Laboratory, as part of a multispecies food-habit study conducted from 1973 through 1976. The sampling area covered the continental shelf waters from Cape Hatteras, N.C., to the Canadian coast of Nova

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[2]Hahm, W., and R. Langton. 1980. Prey selection based on predator/prey weight ratios for some northwest Atlantic fish. Int. Counc. Explor. Sea, C.M. 1980/L:62, 9 p.

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Scotia. Details of this food-habit survey were described in an International Council for the Exploration of the Sea document and will not be repeated here (Langton et al. 1980[3]).

Diet overlap, expressed as the percentage similarity between diets, was calculated according to the formula of Shorygin (Ivlev 1961) and has been described in several other papers as a means of evaluating the diet of northwest Atlantic finfish (Langton and Bowman 1980; Grosslein et al. 1980) although there are other methods of indexing like diets (Lipovsky and Simenstad 1978). The calculation is quite simple and is done by summing the smaller value, as a percentage weight in the present case, for all prey shared by the two predators. The computed value ranges from 0 to 100%, with 0% representing no diet overlap and 100% representing identical diets. The final overlap value is sensitive to the taxonomic level at which the prey was identified and for this paper the finest taxonomic breakdown available was used, i.e., prey identified to species whenever possible. Because of the sensitivity of this overlap measure to the taxonomic breakdown of prey, statistical methods of evaluating absolute overlap values are not practical. Instead, the values have been classified as low, 0-29%; medium, 30-60%; or high, >60% for the purpose of discussion.

The computation of diet overlap was automated and the actual computer program checked by running diet overlap for any one predator against itself. In this case the computer generates a value of 100% overlap for fish in the same size class and then a mirror image of values on each side of the 100% line. This is shown graphically in Figure 1 where Atlantic cod is plotted three dimensionally versus Atlantic cod. The plotting program only considered size classes up through class 25 (125 cm maximum fork length), but by truncating the output at this level little data was eliminated (a total of 5 cod out of 1,714 examined, for example). In fact, since the fish were taken randomly from the catch, the majority of the samples came from the most frequently occurring size classes which, even for Atlantic cod, did not approach this maximum size. Furthermore, size classes that did not include a sample size of at least 10 fish were eliminated before the data were plotted since very small samples would not necessarily be representative of the size class.

This study concentrates on two of the major fish predators in the northwest Atlantic, silver hake and Atlantic cod, and on the questions of their diet overlaps with 15 other finfish species. The food habits information presented is limited to an explanation of the prey shared by the predators which results in the observed overlap values. Detailed descriptions of the diet of the fish collected by the Northeast Fisheries Center are in preparation or have been given elsewhere. Dietary information on the northwest Atlantic Gadiformes and Pleuronectiformes can, for example, be found in Langton and Bowman (1980, 1981), Bowman and Bowman (1980), and Durbin et al. (1980)[4] while data on fish from other taxa are described in Edwards and Bowman (1979) and Grosslein et al. (1980).

RESULTS

Atlantic Cod — Little Skate

Atlantic cod, *Gadus morhua* Linnaeus, and little skate, *Raja erinacea* Mitchell, show relatively little similarity in diet (Fig. 2A). The maximum value of 48% was found for the overlap between size class 3 (11-15 cm) Atlantic cod and size class 3 little skate. The prey shared by these predators are primarily small crustaceans, in particular amphipods such as *Unciola*. Unfortunately, slightly more than 10% of the diet of each of these fish was unidentifiable with a resulting increase in the overlap values. As can be seen from Figure 2A, apart from the peak of 48%, medium levels of dietary overlap exist between Atlantic cod 11-20 cm (size classes 3 and 4) and little skate up to 45 cm total length (size class 9). Medium overlap values again occur between little skate 36-55 cm (size classes 8-11) and Atlantic cod 31-65 cm (size classes 7-13). This overlap can generally be attributed to the preponderance of a variety of crustaceans in the diet of both predators. For larger Atlantic cod the overlap values with little skate are extremely low, primarily because of a

[3]Langton, R., B. North, B. Hayden, and R. Bowman. 1980. Fish food habit studies-sampling procedures and data processing methods utilized by the Northeast Fisheries Center, Woods Hole Laboratory, U.S.A. Int. Counc. Explor. Sea, C.M. 1980/L:61, 16 p.

[4]Durbin, E., A. Durbin, R. Langton, R. Bowman, and M. Grosslein. 1980. Analysis of stomach contents of Atlantic cod (*Gadus morhua*) and silver hake (*Merluccius bilinearis*) for the estimation of daily rations. Int. Counc. Explor. Sea, C.M. 1980/L:60 (revised), 21 p.

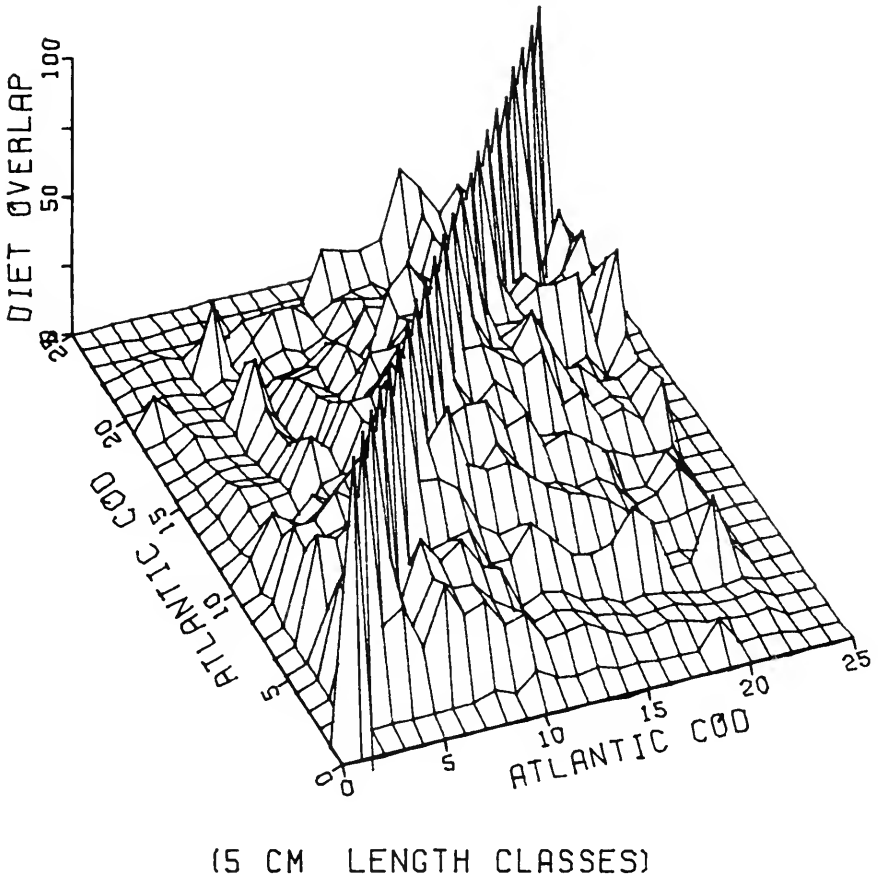

FIGURE 1.—Three dimensional plot of the diet overlap of Atlantic cod versus Atlantic cod; the same data set. Presented here is an example of the graphics output from diet similarity calculations. The peak represents 100% overlap for the same 5 cm length class of fish with a mirror image of values on either side of the peak.

shift in the diet of Atlantic cod from crustaceans to fish.

Atlantic Cod — Redfish

Atlantic cod and redfish, *Sebastes marinus* (Linnaeus), generally show low levels of diet overlap (Fig. 2B). There were, however, some medium overlap values occurring between the smaller Atlantic cod and redfish. The peak value of 49% occurred between redfish 16-20 cm (size class 4) and Atlantic cod 6-10 cm (size class 2) which was primarily the result of predation on pandalid shrimp *Dichelopandalus leptocerus*. Unfortunately, few of the redfish stomachs examined in this size class contained prey (2 out of 21 examined) so this peak may be artificially high, although in the other cases where medium overlap levels were found, pandalid shrimp were generally consumed by both predator species.

Atlantic Cod — Longhorn Sculpin

The pattern of diet overlap between Atlantic cod and longhorn sculpin, *Myoxocephalus octodecemspinosus* (Mitchill), shows low to medium overlap values over much of the size range of both species. The values do decrease, however, between the larger Atlantic cod (>61 cm, size class 13) and smaller longhorn sculpin (<16 cm, size class 3) (Fig. 2C). The peak value of 38% occurred between two different predator size classes, and in both instances the single most important prey contributing to this overlap was the

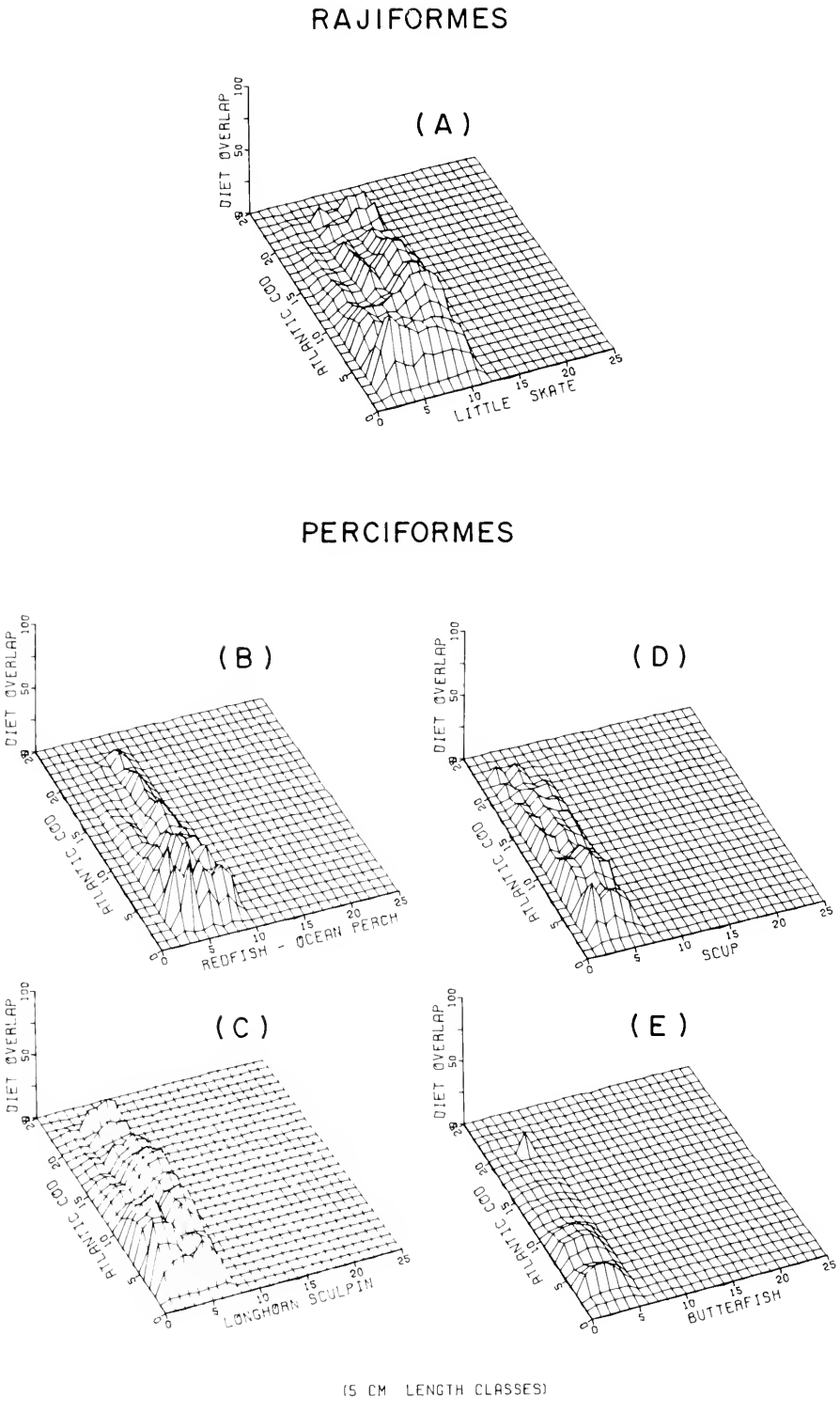

FIGURE 2.—Three dimensional plot of the diet overlap of Atlantic cod with selected rajiform and perciform fishes.

pandalid shrimp *Dichelopandalus leptocerus*, although a large variety of other crustaceans contributed to both of the predator's diets.

Atlantic Cod — Scup

Overlap between the diet of Atlantic cod and scup, *Stenotomus chrysops* (Linnaeus), is at a low level (Fig. 2D), and the low values represent a broad array of prey, principally crustaceans, that constitutes the forage base of these two predators. The only trend in these values is that they are at their lowest for large Atlantic cod (>80 cm) and all size classes of scup. This is the result of the larger Atlantic cod's piscivorous habits.

Atlantic Cod — Butterfish

The Atlantic cod and butterfish, *Peprilus triacanthus* (Peck), show very low diet overlap levels, the maximum being 19% for 11-15 cm (size class 3) fish of both species. There was, however, relatively more overlap between the smaller Atlantic cod (<45 cm) and all sizes of butterfish sampled (Fig. 2E).

Atlantic Cod — White Hake

The diet of white hake, *Urophycis tenuis* (Mitchill), shifts from crustaceans such as euphausiids, shrimp, and mysids when they are small (<≅50 cm) to primarily fish for the larger white hake. This parallels the change in the Atlantic cod's diet with size. The result is a varying degree of dietary overlap across all size classes of fish examined (Fig. 3A). Low levels occurred between the smaller white hake and the larger size classes of Atlantic cod and vice versa. Intermediate levels, values in the 30-50% range, are found in clusters which are the result of a variety of shared prey types. Some of these values in the 40 and 50% range depend upon the fish components in the diet. In particular, silver hake and herring, *Clupea harengus*, together with unidentified fish are the most commonly occurring prey that these predators share. The greatest overlaps observed were between 21-25 cm (size class 5) Atlantic cod and several larger size classes of white hake (36-85 cm, size classes 8-17) (Fig. 3A). This high overlap is somewhat artificial since it is the result of unidentified fish prey in both predators' diets. It does, however, amplify the importance of fish prey to these predators.

Atlantic Cod — Red Hake

Atlantic cod and red hake, *Urophycis chuss* (Walbaum), have low to intermediate levels of diet overlap. The lowest values occur between small red hake and large Atlantic cod (Fig. 3B). These small red hake prey quite heavily on crustaceans while the larger Atlantic cod have shifted their habits from crustacean prey to fish. The diet of red hake does, however, include more fish prey as the predators themselves grow, so that the overlap values between the larger size classes of red hake and Atlantic cod remain at an intermediate level.

Atlantic Cod — Spotted Hake

Atlantic cod and spotted hake, *Urophycis regia* (Walbaum), have diets which overlap at low to intermediate levels (Fig. 3C). The prey that they have in common is primarily crustaceans but may also include some fish. The cluster of intermediate values occurring between 11-25 cm (size classes 3-5) Atlantic cod and 11-30 cm (size classes 3-6) spotted hake is, for example, the result of predation on crustaceans such as *Meganyctiphanes*, *Dichelopandalus*, *Crangon*, *Unciola*, and other less significant taxa, while the intermediate overlap peaks between 31-35 cm spotted hake and Atlantic cod are due to fish predation.

Atlantic Cod — Pollock

Atlantic cod and pollock, *Pollachius virens* (Linnaeus), show low to intermediate levels of diet overlap over all size classes of both predators examined. Both of these species are crustacean/fish predators, relying more heavily on fish as they increase in size. For the smaller pollock, the euphausiid *Meganyctiphanes norvegica* and the shrimp *Pasiphaea multidentata* were the major components of the diet while the Atlantic cod relied on a much broader variety of prey. For the larger fish of both species a variety of pisces were included in the diet, some of which was not readily identifiable at any lower level than simply fish flesh. The problem in identifying fish remains generated two artificial peaks in overlap

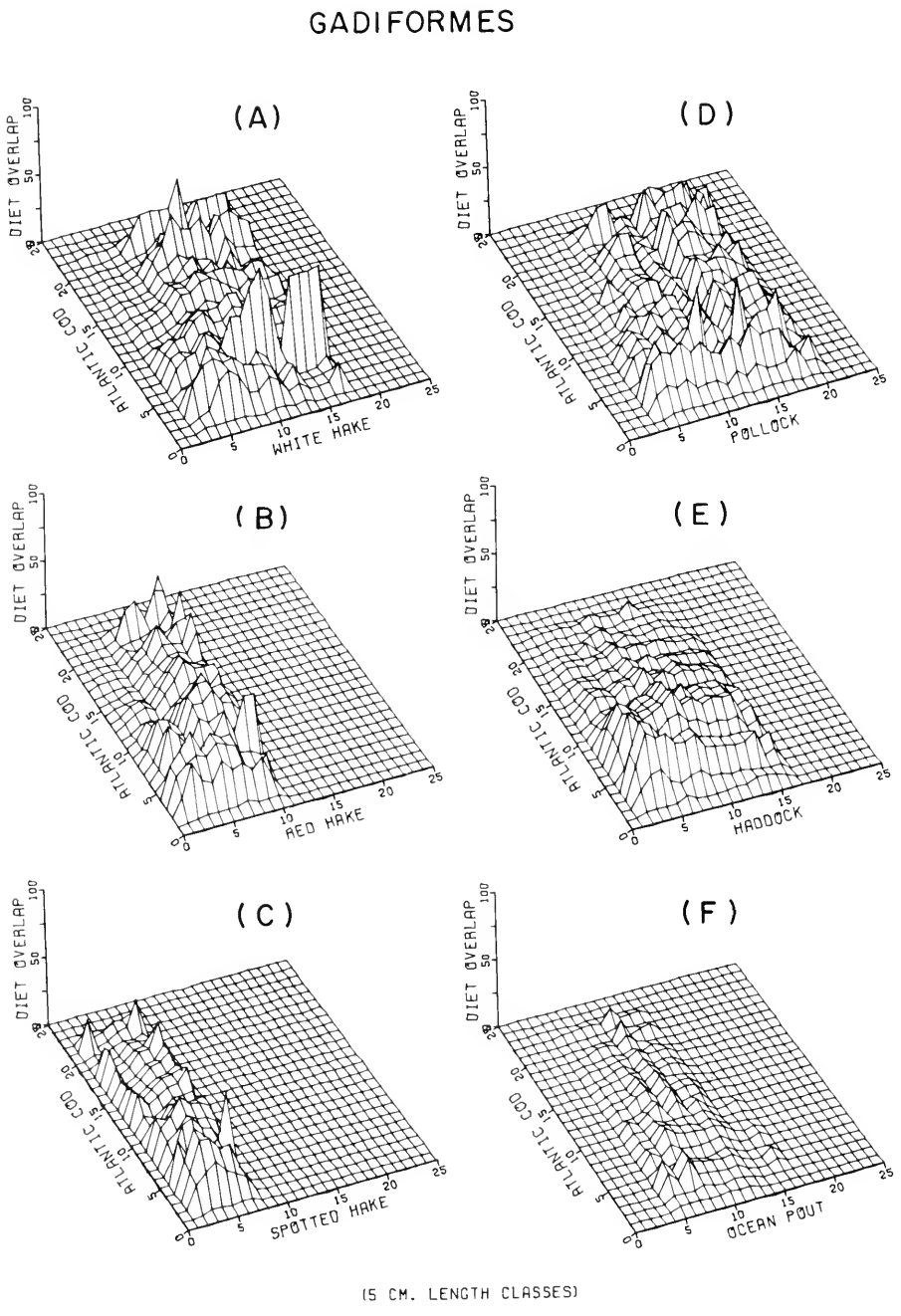

FIGURE 3.—Three dimensional plot of the diet overlap of Atlantic cod with selected gadiform fishes.

between Atlantic cod of size class 5 and pollock of size classes 10 and 14 as seen in Figure 3D.

Atlantic Cod — Haddock

Haddock, *Melanogrammus aeglefinus* (Linnaeus), is primarily benthic in its feeding habits with the result that its diet is similar to Atlantic cod's only when the Atlantic cod are also feeding on the benthos. Consequently, the degree of diet overlap between these two predators is highest for the smaller animals, as can be seen in Figure 3E. The diversity of prey that both these predators consume reduces the computed overlap values. The relatively low maximum values, 47% being the highest for 16-20 cm (size class 4) Atlantic cod and 11-15 cm (size class 3) haddock, make it difficult to identify any particular species of prey that gives rise to the observed intermediate levels of overlap.

Atlantic Cod — Ocean Pout

Ocean pout, *Macrozoarces americanus* (Schneider), are fairly specific in their predatory habits, and these habits do not overlap with those of Atlantic cod to any extent (Fig. 3F). A single prey species, the sand dollar, *Echinarachnius parma*, accounts for most of the diet of ocean pout although amphipods were also present in many of the fish stomachs examined.

Atlantic Cod — American Plaice

The diets of Atlantic cod and American plaice, *Hippoglossoides platessoides* (Fabricius), overlap at quite low levels, the highest value being 33% for 26-30 cm (size class 6) Atlantic cod and 21-25 cm (size class 5) American plaice. American plaice prey on a variety of benthic animals but, as they grow larger, they rely more on echinoderms than crustaceans and polychaetes. This is reflected in the diet overlap plot (Fig. 4A); the larger size classes of American plaice (>45 cm) have extremely small overlap with Atlantic cod because of predation on the sand dollar.

Atlantic Cod — Witch Flounder

Little diet overlap occurs between Atlantic cod and witch flounder, *Glyptocephalus cynoglossus* (Linnaeus), with all of the calculated values being 30% or less (Fig. 4B). Witch flounder are benthic predators with polychaete worms being of major importance as prey although they do consume crustaceans and other invertebrates. It is the crustacean component of the diet which accounts for these low levels of overlap with the Atlantic cod.

Atlantic Cod — Yellowtail Flounder

The diets of Atlantic cod and yellowtail flounder, *Limanda ferruginea* (Storer), overlap at generally low levels (Fig. 4C). There is only one cluster of intermediate levels involving yellowtail flounder from a single size class (class 3, 11-15 cm) which reflects the occurrence of pandalid shrimp *Dichelopandalus leptocerus* in both predators' diets. As with many other species, a reduction in the level of overlap occurs as the disparity in fish size increases. For yellowtail flounder this is quite apparent when compared with the larger Atlantic cod because the large Atlantic cod are primarily piscivorous. However, this reduction is not as noticeable for large yellowtail flounder and small Atlantic cod since the benthic habits of yellowtail flounder change little as the fish increase in size.

Atlantic Cod — Fourspot Flounder

Atlantic cod and fourspot flounder, *Paralichthys oblongus* (Mitchill), show low and intermediate levels of diet overlap (Fig. 4D) which is primarily a result of predation on crustaceans. The single most important crustacean prey was the pandalid shrimp *Dichelopandalus leptocerus* which makes up from 17% to 30% of the diet of 21-30 cm fourspot flounder and 3% to 40% of the diet of 6-45 cm Atlantic cod.

Silver Hake — Little Skate

The pattern of diet overlap between silver hake, *Merluccius bilinearis* (Mitchill), and little skate is shown in Figure 5A. Generally, overlap levels are low but medium levels range up to a high of 44% between small silver hake 1-15 cm (size classes 1-3) and little skate 11-45 cm total length (size classes 3-9). This degree of overlap can be attributed to the crustaceans in each of these predators' diets with the sand shrimp, *Crangon septemspinosa*, being of particular importance. For larger silver hake the diet overlap with little skate is insignificant since these larger hake prey on fish while little skate of all sizes prey primarily on benthic crustaceans.

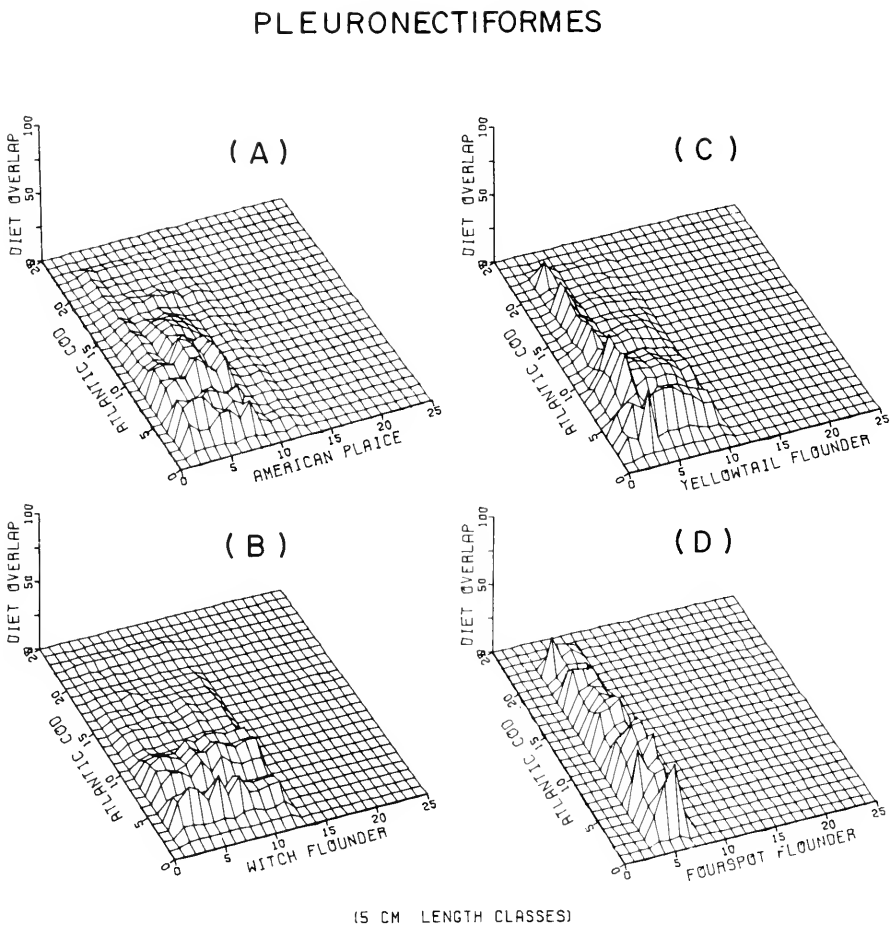

FIGURE 4.—Three dimensional plot of the diet overlap of Atlantic cod with selected pleuronectiform fishes.

Silver Hake — Redfish

High levels of overlap occur between 16-20 cm (size class 4) silver hake and 11-45 cm (size classes 3-9) redfish (Fig. 5B). The peak value is 75% for 31-35 cm (size class 7) redfish and these smaller silver hake. Most of this overlap is due to predation on the euphausiid *Meganyctiphanes norvegica*, which accounted for 60% and 63% of the diet of these 16-20 cm silver hake and 31-35 cm redfish, respectively. The other high overlap values between these two predators can also be attributed to euphausiids making up more than 50% of the diets. Medium levels of overlap, 30-42%, were found for other size silver hake and redfish. Once again *Meganyctiphanes norvegica* was a major dietary item but in some cases *Dichelopandalus leptocerus* also contributed significantly. For the larger silver hake (>35 cm, greater than size class 7) there was little, if any, diet overlap. These large silver hake prey heavily on fish while redfish are predominantly crustacean predators.

Silver Hake — Longhorn Sculpin

Intermediate diet overlap values occur between silver hake ranging from 6 to 15 cm in length (size classes 2-3) and most of the size classes of longhorn sculpins examined (Fig. 5C). This overlap is due to both predators' reliance on crustaceans such as *Crangon septemspinosa*, *Dichelopandalus leptocerus*, and *Neomysis americana*. For the larger silver hake, those that are primarily piscivorous, there is virtually no over-

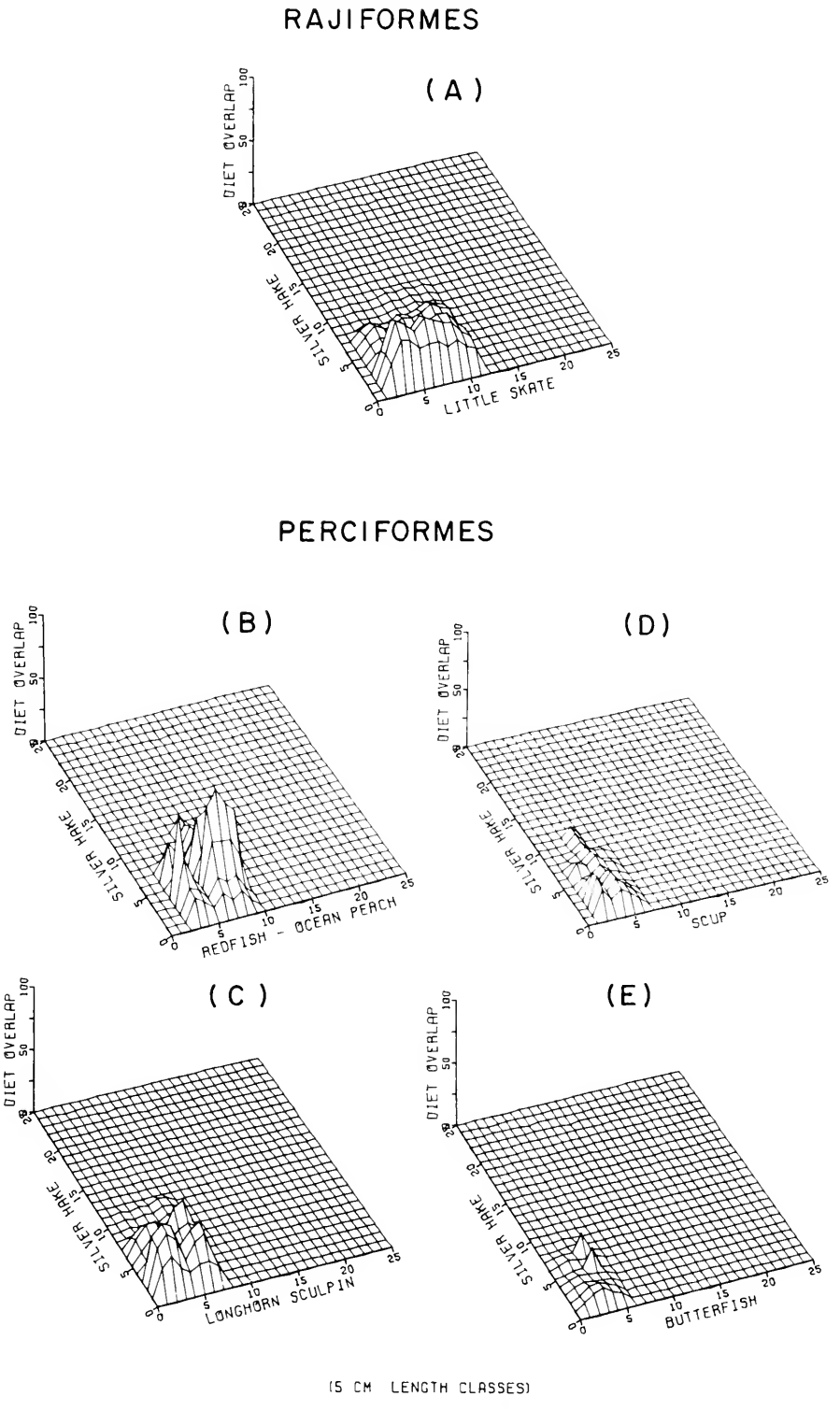

FIGURE 5.—Three dimensional plot of the diet overlap of silver hake with selected rajiform and perciform fishes.

lap or, at least, extremely low levels of overlap with longhorn sculpin.

Silver Hake — Scup

Silver hake and scup both prey on crustaceans, but they share few prey species in common so that diet overlap values are quite low (Fig. 5D). There is a trend for the overlap values to decrease when comparing larger silver hake and scup which mirrors the shift towards fish predation by these larger silver hake.

Silver Hake — Butterfish

The diets of silver hake and butterfish overlap at very low levels, the highest value being 17% which was the result of predation on the squid *Loligo* (Fig. 5E). Generally, the butterfish is more planktonic in its predatory habits than the silver hake which is reflected in the low overlap values.

Silver Hake — Atlantic Cod

Silver hake and Atlantic cod are generally found to have low to intermediate levels of diet overlap and very few values that are >60% (Fig. 6A). All of the high values are the result of unidentified fish remains forcing up the computed overlap values. Both of these predators become more piscivorous as they grow larger, but this size-specific dietary shift is not reflected in an obvious change in the level of diet overlap. In other words, the smaller fish share crustacean prey species such as euphausiids while the larger predators both prey on a number of different species of fish.

Silver Hake — White Hake

There is a clear pattern of overlap when comparing the diets of silver and white hake (Fig. 6B). The diets of the larger fish of both species do not overlap with the smaller fish of the opposite species. In other words, the diet of small silver hake has little in common with the larger white hake and vice versa. The explanation for this is a size dependent change in diet for both predators. When small, they both rely on crustaceans, such as euphausiids, and then gradually shift to fish as the predator grows. For example, the high value, 74% between 16-20 cm (size class 4) silver hake and 31-35 cm (size class 7) white hake results from over 50% of either of these predators feeding on *Meganyctiphanes norvegica*. For comparison, the other high value, 75%, for 41-45 cm (size class 9) silver hake and 66-70 cm (size class 14) white hake, is the result of fish predation on such fish as silver hake, clupeids, and other unidentifiable fish remains.

Silver Hake — Red Hake

The diet overlap between silver and red hake ranges from 0% to intermediate levels as high as 56%. The general pattern is increasing overlap with increasing predator size up to 26-30 cm (size class 6) and then leveling off or decreasing slightly between the larger fish (Fig. 6C). The peak value, occurring between 26-30 cm silver hake and 41-45 cm (size class 9) red hake, can be explained by predation on fish, *Dichelopandalus leptocerus*, and other invertebrates.

Silver Hake — Spotted Hake

Silver and spotted hake show, for the most part, intermediate to high levels of diet overlap between similar size fish (Fig. 6D). Peak values of 60% and 70% occur, for example, between 11-20 cm (size classes 3-4) and 16-25 cm (size classes 4-5) silver and spotted hake, respectively. These peaks are the result of a reliance by both predators on *Meganyctiphanes norvegica*, *Dichelopandalus leptocerus*, and *Crangon septemspinosa*. The intermediate overlap values are also, however, a reflection of predation on fish, especially for the larger silver and spotted hake.

Silver Hake — Pollock

High diet overlap values exist between silver hake 16-20 cm (size class 4) and pollock 16-65 cm (size classes 4-13). Two prey categories are responsible for these high levels, *Meganyctiphanes norvegica* and unidentified fish remains. Medium levels of overlap between these two predators are common for most size classes except for silver hake below 10 cm. Overlap between these smaller silver hake and all sizes of pollock falls into the lower overlap category. There are also extremely low values between small pollock and large silver hake (Fig. 6E).

Silver Hake — Haddock

Silver hake and haddock show little similarity in their diets and the resulting diet overlap val-

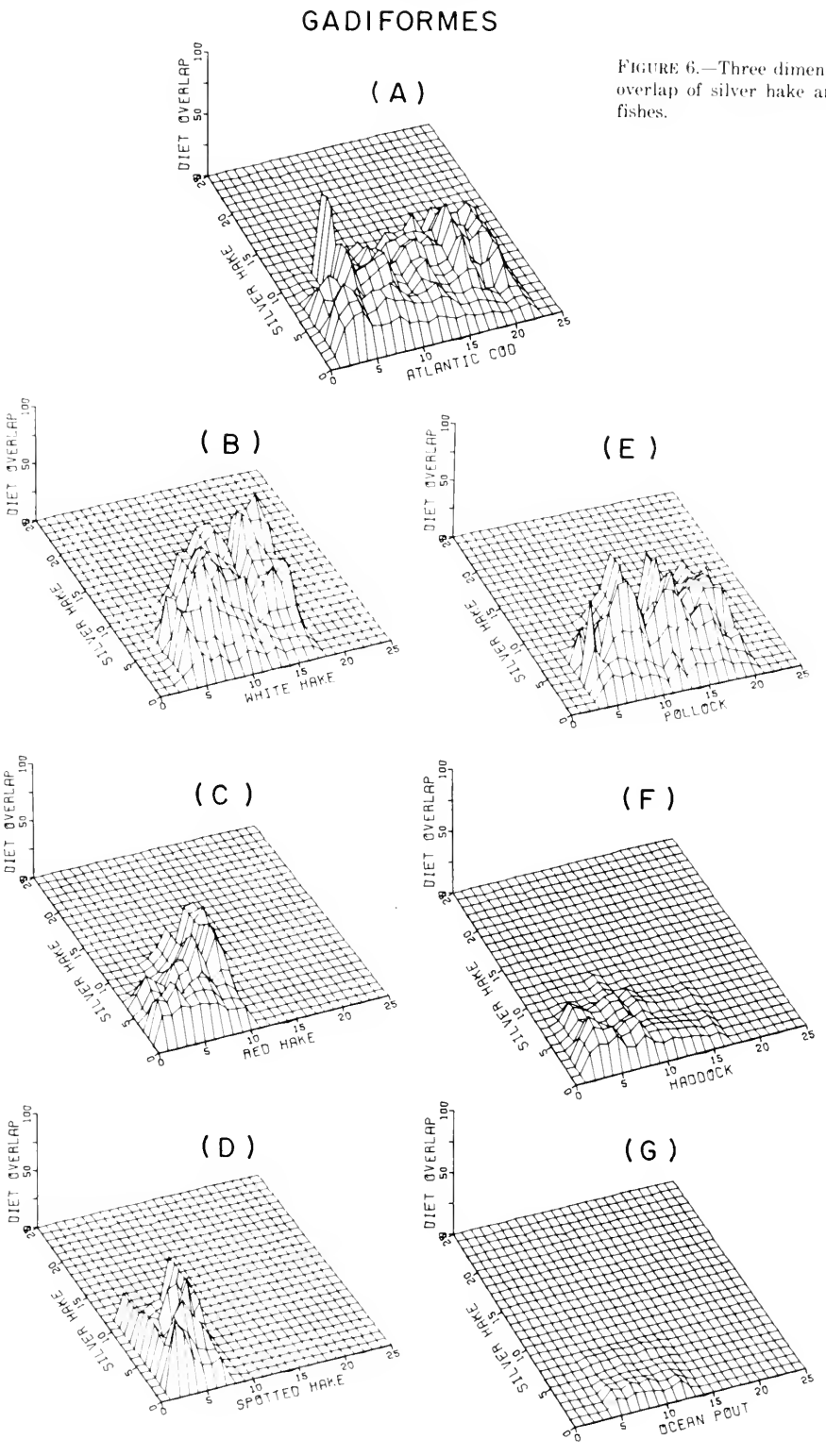

FIGURE 6.—Three dimensional plot of the diet overlap of silver hake and selected gadiform fishes.

ues are all quite low (Fig. 6F). Even with these low values, there is an obvious trend; the higher values occur between the smaller individuals of these two predators which reflects the dependance of small silver hake and haddock on crustacean prey.

Silver Hake — Ocean Pout

The diets of silver hake and ocean pout are mutually exclusive so that there is an extremely small degree of diet overlap (Fig. 6G). The only prey that they share in common are amphipods, but again, this is at a very low level.

Silver Hake — American Plaice

Silver hake and American plaice show very low levels of dietary overlap (Fig. 7A). Despite the lack of diet similarity, a pattern does emerge when comparing these two predators. The larger size classes of both species show virtually no overlap, while what similarity does exist occurs between silver hake and American plaice <40 cm. The diet of these larger individuals is quite specific, fish for silver hake and echinoderms for American plaice, so little overlap is to be expected, while the smaller individuals of both species prey on invertebrates.

Silver Hake — Witch Flounder

Silver hake and witch flounder share little prey in common with resulting low levels of diet overlap. The only exception to these low levels is a high peak (66% and 67%) between 16-20 cm (size class 4) silver hake and 11-20 cm (size classes 3-4) witch flounder (Fig. 7B). A single prey species,

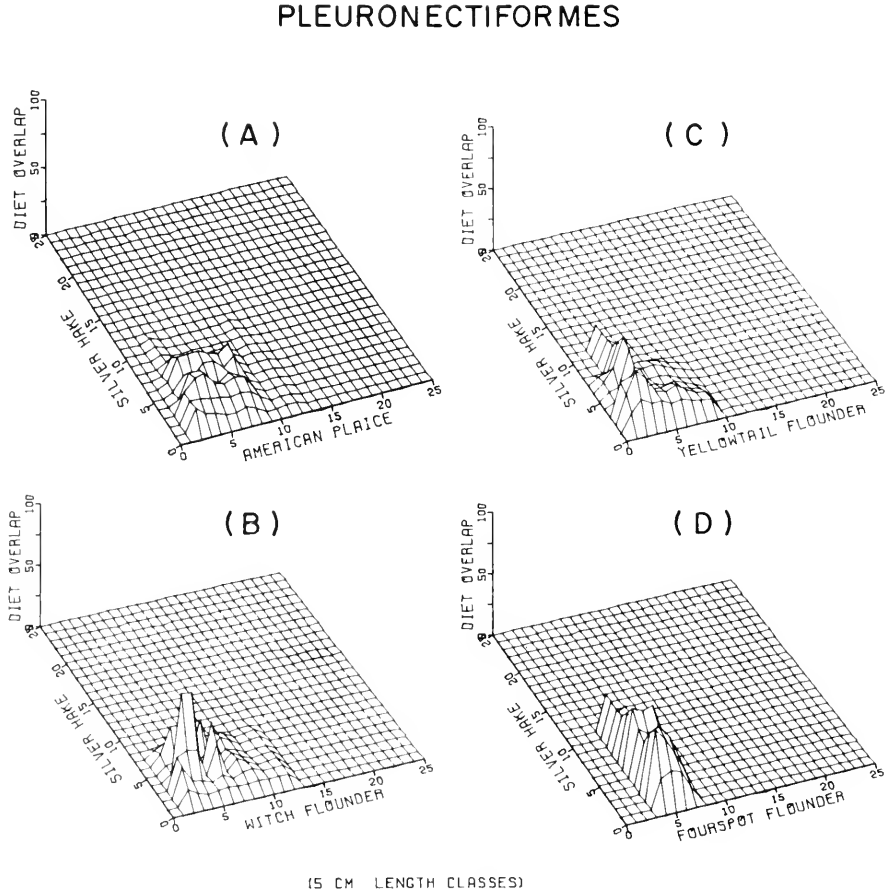

FIGURE 7.—Three dimensional plot of silver hake and selected pleuronectiform fishes.

Meganyctiphanes norvegica, is responsible for this since it alone accounts for >63% of each predator's diet. Similarly, the smaller peaks in the figure are also the result of having euphausiids as a common prey item.

Silver Hake — Yellowtail Flounder

Silver hake and yellowtail flounder have, for the most part, low levels of diet overlap (Fig. 7C). The few intermediate levels that do occur are, in all but one instance, related to yellowtail flounder that are 11-15 cm in length (size class 3) which have preyed on *Crangon septemspinosa*, *Dichelopandalus leptocerus*, or small unidentified fish. The one exception is for 6-10 cm (size class 2) yellowtail flounder and silver hake. These fish preyed primarily on *Crangon septemspinosa*, *Neomysis americana*, and amphipods with a resulting diet overlap of 39%. Even with these low overlap levels an overall pattern is apparent; the greatest overlap occurs between the smaller size classes of both species.

Silver Hake — Fourspot Flounder

The diets of silver hake and fourspot flounder overlap at low to intermediate levels (Fig. 7D). The highest value, 54%, occurs between 6-10 cm (size class 2) silver hake and 16-20 cm (size class 4) fourspot flounder. The peak, as with most of the other intermediate values, is the result of predation on crustaceans such as *Crangon septemspinosa*, *Neomysis americana*, and *Dichelopandalus leptocerus*.

DISCUSSION

The diet overlap comparisons presented here are one way to simplify fish food habits data and to identify real or, at least, potential pathways of energy exchange. As with any method of data reduction, however, certain compromises have to be accepted which must be kept in mind when discussing the results. The limitations of percentage similarity calculations have been described by several authors (Day and Pearcy 1968; Moyle 1977; Keast 1977; Langton and Bowman 1980; MacPherson 1981) and these limits include both biotic and abiotic factors. Such factors as the taxonomic level of prey identification, the actual quantity of prey consumed (especially since percentage similarity is a relative measure of dietary constituents), predator/prey distribution and abundance, and temporal factors that influence both predator and prey behavior all have to be considered in evaluating the meaning of diet overlap data.

The present data consider the entire northwest Atlantic as a single homogeneous ecological system since all the available data were grouped by species for the diet overlap calculations. This is a first attempt to examine size-specific finfish predation in the northwest Atlantic and, without more extensive basic biological information on finfish and invertebrate community structure, there was no reason to subdivide the data set. The research survey cruises on which the fish stomachs were collected were, however, planned for discrete geographic regions (e.g., Gulf of Maine, Georges Bank) and employed stratified random sampling based primarily on depth dependent strata (Grosslein 1969; Clark and Brown 1977). If the research survey catch data were analyzed statistically, using techniques such as cluster analysis, to identify fish species associations or assemblages, then there may be justification for subdividing the data set. Such methods have been utilized recently to identify northwest Pacific finfish assemblages (Gabriel and Tyler 1980; Tyler et al. in press) and have been used, to a limited degree, for northwest Atlantic fishes (Tyler 1972, 1974; Knight and Tyler 1973). Whatever techniques are employed the basic problem is the same: defining what constitutes an ecologically homogeneous system.

From the figures presented, it is clear that completely dissimilar diets occur very rarely. This raises the question of the significance of diet overlap and whether such measures are indicative of resource competition. The limits of diet overlap calculations have been dealt with briefly above and the significance of any given numerical value for diet overlap has also been mentioned. Diet overlap has some value as an indicator of potential energy flow pathways but it is not an absolute measure of trophic linkages. The overlap values are obviously indicators of coexistence rather than competition, especially since overlap values have been observed to decrease rather than increase when resources are limited (Zaret and Rand 1971; Keast 1978; MacPherson 1981). The ideas of competition versus coexistence have been considered for gadoid fishes by Jones (1978). Jones pointed out some of the more subtle distinctions between the diets of three gadoid species which, on cursory examination, appear to overlap. For example, although

both haddock and Atlantic cod from the same trawl haul preyed on juvenile *Sebastes*, they were preying on different-sized juveniles and, in general, Jones observed that Atlantic cod tended to consume larger prey than haddock of the same size. This type of detailed stomach contents analysis, together with observations on fish feeding behavior in the laboratory and in situ, is the type of biological information necessary for accurately defining what constitutes an ecologically homogeneous system, or, more importantly, an energetically coupled unit within the system.

There are some general patterns to the overlap values which may indicate real, or at least potential, trophic linkages. In comparing Atlantic cod with six other gadids, for example, the overlap levels generally are at their lowest between the larger cod (greater than size class 10, >50 cm) and the smaller size classes of the other predators (Fig. 3). This reflects the shift in the Atlantic cod's feeding habits from being primarily a crustacean predator to a piscivore with an increase in body size. In effect, Atlantic cod occupy different, size-specific, feeding niches which correspond to these other predators only when both species are small and more dependent on crustacean prey. For silver hake (Fig. 6) the pattern is similar but silver hake are a smaller fish than Atlantic cod and switch to a piscivorous habit at a smaller size. In addition to this pattern, there is also a noticeable shift in overlap between silver hake, the three other hake species, and pollock. The overlap with the smaller size classes of silver hake is low or even decreases slightly as the four other gadid species increase in size. Conversely, overlap is highest for the larger silver hake and these four gadids. This is a result of predation on many different species of crustaceans by all these predators and a shift towards fish predation as they grow.

In comparing both Atlantic cod and silver hake with the one rajiform and the four perciform fish species, the overall pattern of diet overlap is the same. The larger Atlantic cod and silver hake show a decreasing level of overlap with the smaller size classes of these other finfish predators (Figs. 2, 5). Atlantic cod and silver hake do not show a similar pattern of diet overlap when compared with the four pleuronectiform species of finfish (Figs. 4, 7). With the three pleuronectid species (Fig. 4A-C) the highest levels of overlap with Atlantic cod occur between the smaller size classes of all three species while the lowest levels occur between the larger size classes. This is similar to changes in overlap observed for the perciform species. For the one bothid (Fig. 4D) a size-dependent shift in overlap is not readily apparent. The overlap values for silver hake and flatfishes are at a maximum, albeit low overall, for the smaller individuals of the three pleuronectids (Fig. 7A-C) but, like the Atlantic cod, are fairly constant over all size classes of the one bothid species examined (Fig. 7D). This pattern of diet overlap with the pleuronectids may be attributed to the crustacean/fish shift in diet for the Atlantic cod and silver hake, and either little change in the flatfish diet or, as with American plaice, a change in diet to one that does not include much, if any, fish prey.

Atlantic cod and silver hake are crustacean/fish predators with a size-dependent shift in predation from crustaceans to fish as these predators grow. In the present data the shift to fish predation for Atlantic cod occurs at about 60-70 cm and for silver hake at about 20-25 cm. These sizes are not absolute and depend very much on the availability of prey. Daan (1973), for example, observed a difference in North Sea cod feeding habits when comparing samples from the northern and southern North Sea. Crustaceans predominated in the stomachs of the larger specimens from the southern region while their northern counterparts had already shifted over to a piscivorous habit. In the northwest Atlantic a similar, but less obvious, shift was observed in the diet of cod when compared over a 10-yr period (Grosslein et al. 1980). When the finfish biomass was low (1973-76 vs. 1963-66), crustaceans were slightly more important as prey although the general impression resulting from studying the two data sets was a fairly constant pattern of predation over time. The diets of Atlantic cod, and presumably most of these other predators, are fairly stable although there is an apparent degree of fine tuning that depends upon the availability of prey and other controlling factors in the environment.

In summary, assuming that the diets of Atlantic cod and silver hake are reasonably stable over time, and that the same is true for the 15 other predators examined, then the pattern of overlap described above suggests that the greatest overall potential for interaction exists between the smaller stages of the two gadids and the other predators. Furthermore, the greatest overlap, with few exceptions, occurs among the gadiform fishes themselves rather than between the gadids and the other ordinal taxonomic levels.

This observation may not only be reassuring to the taxonomist but is also of significance to fishery biologists in their attempts to identify ecological units. It suggests that future food habit studies should be directed towards the juvenile, or at least smaller, stages of closely related species if the goal is to understand how finfish coexist by partitioning food resources in the marine environment.

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THE RELATIONSHIP OF WINTER TEMPERATURE AND SPRING LANDINGS OF PINK SHRIMP, *PENAEUS DUORARUM*, IN NORTH CAROLINA[1]

WILLIAM F. HETTLER AND ALEXANDER J. CHESTER[2]

ABSTRACT

Spring landings of pink shrimp in North Carolina were highly correlated with water temperature during the previous winter. The strongest relation was found between landings and the average water temperature of the two coldest consecutive weeks of each year ($r^2 = 0.82$). Following the cold winters of 1977, 1978, 1980, and 1981, when temperatures averaged below 5°C, landings were <160,000 kg. Following the warm winters of 1965, 1974, and 1975, when temperatures averaged above 8°C, landings were >450,000 kg. Changes in water temperature through the year were described by a sine-cosine curve in which minimum temperatures generally occurred during the 5th week and maximum temperatures occurred during the 31st week of the year. Weekly mean air temperatures were linearly related to water temperatures ($r^2 = 0.97$) over the entire range of data, but they were not useful as proxy data for predicting pink shrimp landings ($r^2 = 0.50$) because the air-water relation was more variable at low temperature. Local rainfall did not have a significant effect on shrimp landings.

Temperature is a critical environmental factor influencing metabolism, growth, reproduction, distribution, and survival of animals (Kinne 1963). Local abundance may be affected by migration or death in response to extreme deviations from temperatures to which the animal is adapted. The effect of such temperature extremes is expected to be more severe for a population at the limit of its geographic range, particularly when temperature is known to be a factor limiting north-south distribution (Williams 1969a).

For species whose life cycle is completed in 1 yr, or in fisheries where reliance on annual recruitment is heavy (Loucks and Sutcliffe 1978), temperature records may be useful as a predictor of landings. A cause-and-effect relationship between harvest and temperature may be more obvious for species with one year class than for long-lived species whose landings are complicated by multiple year-class contributions (Norcross and Austin 1981). Penaeid shrimp, which have an annual life cycle, have no significant contribution from other year classes to compensate for a reduction in biomass caused by unfavorable temperatures.

Shrimp mortality in the southeast United States due to cold has been reported by Gunter and Hildebrand (1951), Lindner and Anderson (1956), and Lunz (1958). Of the three species of *Penaeus* that occur in North Carolina waters, only pink shrimp, *Penaeus duorarum* Burkenroad, overwinter in shallow estuaries (Williams 1955a) and, therefore, would be more likely to suffer from abnormally cold winter temperatures than either brown shrimp, *P. aztecus*, or white shrimp, *P. setiferus*. Pink shrimp have an annual life cycle in which the adults spawn offshore during early summer and postlarvae and juveniles utilize the estuaries, where several environmental factors can affect distribution and survival. These factors include temperature, salinity, substrate, debris cover, and seagrass species and density (Costello and Allen 1970; Grady 1971; Gunter 1950, 1961; Williams 1955a, 1958, 1969b). Peak recruitment of postlarvae into North Carolina estuaries occurs from July to September (Williams 1969b). Juveniles that overwinter in the estuary migrate towards the sea as adults, primarily in May and June, and become the object of a trawl and channel net fishery located in the mouth of the Neuse River, southwestern Pamlico Sound, Core Sound, Bogue Sound, and in the ocean between Beaufort Inlet and Bogue Inlet (Williams 1955b).

The primary purpose of this study was to investigate the relationship between winter tem-

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peratures and spring landings of pink shrimp in North Carolina to determine if temperature could be used as a predictor of landings. Several recent harsh winters (Diaz and Quayle 1980; Ingham 1979) provided an opportunity to compare landings over a range of temperatures. This relationship may serve to focus attention on the importance of temperature extremes in understanding ecosystem productivity. We also analyzed available water and air temperatures to model the annual temperature in the lower Newport River estuary, to compare the weekly mean temperatures of each year with the annual model, and to test the use of air temperature as proxy data for periods when no water temperatures were available. Finally, we examined the effect of local winter rainfall on pink shrimp landings.

METHODS

Temperature records were analyzed from the Newport River estuary, which is centrally located within the North Carolina pink shrimp nursery and fishing grounds, the "Carteret-Onslow Area" of Williams (1955b) (Fig. 1). This estuary had been the site of several studies conducted by our laboratory during which temperatures were routinely monitored at one or more locations, but the entire time-series of temperature records had not been analyzed.

Seawater temperatures were obtained from recordings made at Pivers Island near Beaufort, N.C., at the mouth of the Newport River estuary beginning in 1962. From 1962 until 1968, records were kept on the island's north channel, and from 1968 to the present, records were kept on the east channel. These locations are <400 m apart. From 1968 to mid-1974, continuous records either were not kept or were inadvertently lost. Thus, complete continuity from 1962 to 1981 was not possible.

Seawater temperature was recorded continuously on 7-d circular charts. Recordings since 1974 were calibrated (±0.1°C) with a precision mercury thermometer. The accuracy and precision of pre-1974 records could not be determined. Weekly means from 1962 to mid-1974 were calculated by averaging hourly readings during each 7-d cycle. Weekly means from mid-1974 to 1981 were calculated by using a compensating polar planimeter. The planimeter method permitted rapid integration of the entire weekly temperature record into a single temperature by converting the mean radius of the area encompassed by the temperature cycle to the equivalent weekly mean temperature.

Daily air temperatures and monthly precipitation totals were recorded at the National Weather Service observation station in Morehead City, N.C., 6.2 km west of Pivers Island, and were pub-

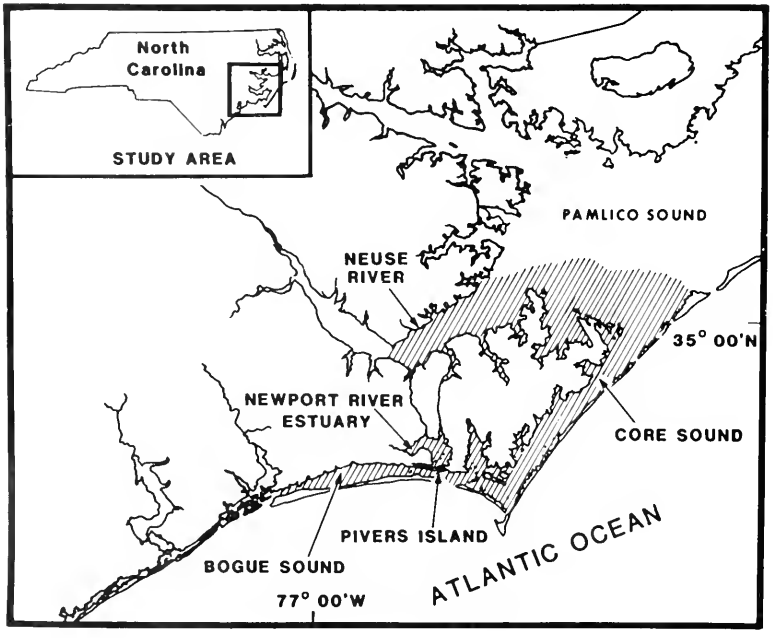

FIGURE 1.—Pink shrimp nursery area (indicated by hatched lines). Pivers Island was point-source of water temperature data.

lished by NOAA Environmental Data and Information Service, National Climatic Center, Asheville, N.C. Weekly mean air temperatures were calculated by averaging daily maximum and minimum records. Rainfall records for December, January, and February were totalled for each winter.

The commercial landings of pink shrimp (kilograms of abdomens) were obtained from records published by the U.S. Department of Commerce (North Carolina Shrimp Landings, Current Fisheries Statistics series) (Table 1). Landings from late winter through July of each year comprised the portion of the fishery considered by our hypothesis to be influenced by severe overwintering conditions, primarily extensive periods of low temperatures and, possibly, reduced salinities. Landings after July were excluded because, in late summer, size and weight decreased, reflecting recruitment of postwinter juveniles into the estuary.

RESULTS AND DISCUSSION

Annual Temperature Cycle in the Newport River Estuary

Weekly mean water temperatures in the Newport River estuary displayed a basically sinusoidal annual pattern (Fig. 2). Actually there appeared to be a slight distortion in the seasonal sine relationship whereby vernal warming proceeded at a slower rate than autumnal cooling. Available data from 1962 to 1981 were used to mathematically define the annual temperature cycle according to the following least-squares, multiple regression equation:

$$T_W = a + b_1 \text{ SIN}\left(\frac{2\pi W}{52}\right) + b_2 \text{ COS}\left(\frac{2\pi W}{52}\right),$$

where T_W was the mean weekly temperature for week W, a was an intercept reflecting the overall average yearly temperature, and b_1 and b_2 were regression coefficients controlling the timing and amplitude of annual minimum and maximum temperatures.

The derived equation (Fig. 2) was an adequate representation of the annual cycle of temperature in the Newport River estuary ($R^2 = 0.93$) and helped illustrate several aspects of the plotted data. Minimum temperatures tended to occur during the 5th week of the year (early February); maximum temperatures occurred during the 31st week (mid-August). Winter temperatures were characterized by greater week-to-week variability than summer temperatures. In general, the fitted curve consistently overestimated winter temperatures. This trend arose from an apparent asymmetry of the minimum and maximum temperatures about the yearly mean. That

TABLE 1.—Landings of pink shrimp in North Carolina compared with various combinations of winter water temperature data collected at Pivers Island, N.C., and air temperature and rainfall data collected at Morehead City, N.C. Air temperature biweekly periods corresponded with the coldest two consecutive weeks used for water temperature.

Year	Landings Feb.-July (kg, heads off)	Average water temperature (°C)				Average coldest biweekly air temp. (°C)	Total rainfall (cm, Dec.-Feb.)
		Dec.-Mar.	Jan.-Feb.	Coldest week	Coldest two consecutive weeks		
1962	365,390	8.5	8.1	6.2	7.0	8.5	20.3
1963	70,237	7.5	7.0	5.9	6.0	5.5	34.4
1964	274,298	8.1	8.3	6.1	6.2	3.2	39.7
1965	452,246	9.9	9.7	7.1	8.4	—	18.0
1966	150,080	9.0	8.2	4.3	5.2	2.9	27.2
1967	387,773	9.0	8.9	6.9	7.6	8.9	33.7
1968	266,781	—	—	—	—	—	27.7
1969	321,693	—	—	—	—	—	21.2
1970	91,968	—	—	—	—	—	32.8
1971	353,767	—	—	—	—	—	31.7
1972	205,667	—	—	—	—	—	41.1
1973	330,455	9.7	8.7	4.7	5.6	3.6	35.5
1974	518,670	12.1	12.6	7.9	9.1	8.8	49.3
1975	497,163	11.6	11.6	10.2	10.6	8.4	34.7
1976	367,671	10.6	9.6	6.0	7.6	4.4	26.7
1977	13,272	6.4	4.9	2.8	3.1	1.0	28.2
1978	15,567	6.9	6.2	3.5	3.8	4.6	37.8
1979	293,432	8.8	7.6	5.6	5.6	3.8	47.6
1980	157,781	8.4	8.2	3.8	4.8	4.8	29.9
1981	134,626	7.8	7.0	3.7	4.9	2.8	36.7
r^2		0.790	0.804	0.720	0.822	0.50	0.003

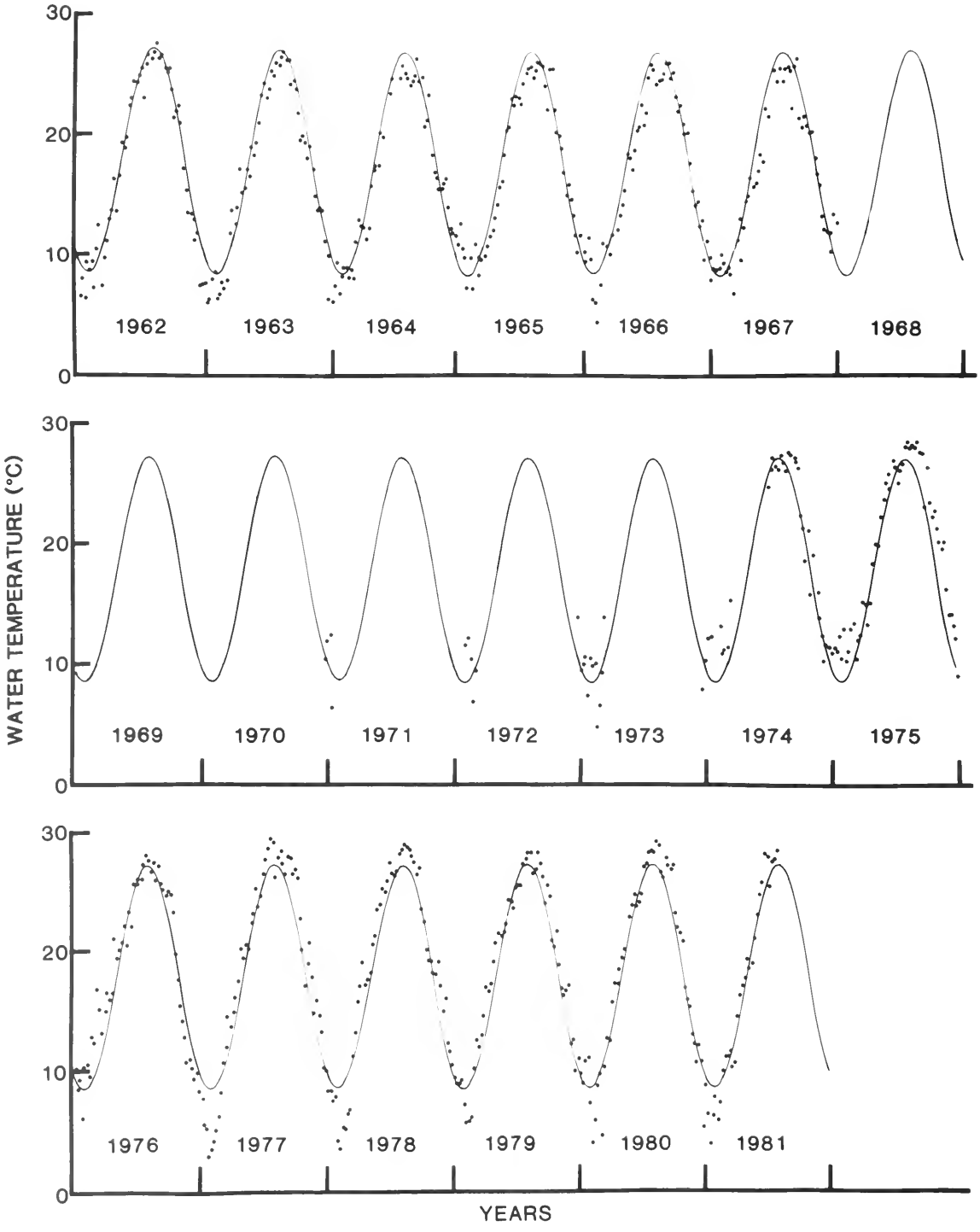

FIGURE 2.—Newport River estuary (Pivers Island) weekly mean water temperatures. Fitted line represents the least squares determined equation: $T_W = a + b_1 \sin\left(\frac{2\pi W}{52}\right) + b_2 \cos\left(\frac{2\pi W}{52}\right)$, where T_W is the mean weekly temperature for week W, $a = 17.88$, $b_1 = -5.20$, and $b_2 = -7.94$ ($R^2 = 0.93$).

is, winter lows were displaced farther from the mean than were summer highs.

As a group the years 1962-67 were cooler in the summer and warmer in the winter than 1974-81. Lower temperatures during cold months reflected a series of very cold winters in the mid-1970s (Diaz and Quayle 1980). An analysis of covariance showed that the average yearly temperature of the 1962-67 year group was significantly different ($P<0.05$) from the 1974-81 group. Either a systematic calibration bias was introduced by different observers, thermographs, and recording locations, or temperatures were actually more extreme in the latter year group. Calibration bias does not satisfactorily explain how both high and low temperature extremes could occur, but a climate phenomenon can be cited. According to R. G. Quayle, NOAA National Climatic Center, Asheville, N.C., the 1962-67 winters were less variable in daily temperature means than the 1973-81 winters. For example, the January and February monthly mean air temperatures at Wilmington, N.C., and Cape Hatteras, N.C., were not different between the two year-groups, but the standard deviations of the monthly means were significantly different at both stations between year-groups (Table 2). Thus, our recorded depressions in weekly winter temperatures in the 1973-81 group probably reflect more extreme actual fluctuations.

TABLE 2.—Comparison of means and standard deviations of January and February air temperatures at two North Carolina coastal stations for year-groups 1962-67 and 1973-81.

Year-group	Air temperature (°C)			
	Wilmington		Cape Hatteras	
	$\bar{X}$	SD	$\bar{X}$	SD
1962-67				
Jan.	7.67	1.51	7.56	1.17
Feb.	8.44	1.73	7.06	1.16
1973-81				
Jan.	7.94	3.74	7.61	3.26
Feb.	8.00	3.10	6.83	3.20

Air-Water Temperature Relation

Close thermal coupling between air and water has been found in shallow estuaries. Roelofs and Bumpus (1953) reported that water temperature in Pamlico Sound showed a seasonal cycle closely related to air temperature. Lindner and Anderson (1956), documenting a winter kill of white shrimp in south Atlantic and Gulf of Mexico waters of the United States, also referred to a close relationship between air temperature and surface water temperature. Smith and Kierspe (1981) presented a model of air-water heat exchanges in a shallow estuary and suggested that their model could reduce the need for in situ instrumentation while providing for close approximation of daily average temperatures.

For the purpose of using air temperatures as proxy data for missing water temperatures (1968-72, Table 1), we decided to examine the relation between local air and water temperatures (Fig. 3). Although air temperature fluctuations were accompanied by a predictable shift in water temperatures over the entire range ($r^2 = 0.97$), at water temperatures below 12°C the relationship was not as useful ($r^2 = 0.68$). We believe that water temperatures rather than air temperatures are required for acceptable predictions of fishery yields in estuaries.

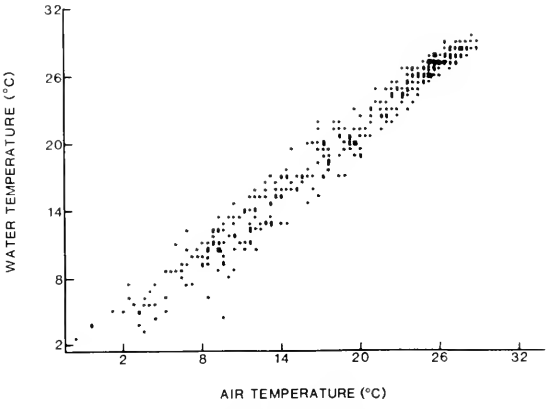

FIGURE 3.—Correlation of Morehead City, N.C., average weekly air temperatures with Newport River estuary (Pivers Island) average weekly water temperatures over 339 consecutive weeks from 1974 to 1981. (Intercept = 2.21, slope = 0.96, $r^2 = 0.97$.) For points below a water temperature of 12°C, $r^2 = 0.68$; and this relationship is not considered useful for predictive purposes during winter.

Relationship Between Temperature, Rainfall, and Pink Shrimp Landings

The February through July pink shrimp landings were considered a dependent variable to be plotted against various combinations of winter temperature data (Table 1). Landings were regressed on average winter water temperature from December through March ($r^2 = 0.79$), average temperature in January and February ($r^2 = 0.80$), average temperature of the coldest week

($r^2 = 0.72$), and average temperature of the two coldest consecutive weeks ($r^2 = 0.82$). All relationships were significant ($P<0.01$). If the average temperature of the two coldest consecutive weeks was <6°C, then shrimp landings were below average (Fig. 4).

Although average winter temperatures (December-March) and average monthly temperatures (January plus February) each accounted for significant portions of the variance in annual landings, the strongest relationship was found between landings and the average of the two coldest consecutive weeks. This may arise because, as Williams (1969b) stated, averages do not adequately represent extremes since they dampen the duration and intensity of the cold. Using a process of expressing temperature in heating degree days, Williams (1969b) postulated that the catch of all species of penaeid shrimps of a given year in North Carolina may depend on net heating degree days during the coldest preceding 6 mo (November-April). He found the poorest catches in cold years (1958, 1961, and 1963) for all three species combined and further suggested that warm years may be as beneficial as cold years are deleterious.

The role of temperature on activity and osmoregulation of pink shrimp has been documented (Williams 1955a, 1960). The lower temperature for activity under experimental conditions was about 14°-16°C; complete cessation of activity was noted below about 10°C. Below 8.8°C, osmoregulatory ability was impaired. Pink shrimp may survive periods of winter cold by burying deeply into the substrate, and Fuss and Ogren (1966) reported that below 14°C, shrimp remain buried, abandoning the usual pattern of nocturnal emergence. Laboratory experiments showed pink shrimp to be more tolerant to combinations of low salinity and low temperature than brown shrimp, and this may explain the occurrence of pink shrimp in North Carolina estuaries during the winter (Williams 1960). In contrast, fall and midwinter brown shrimp immigrants do not survive cold weather as well. The usual recruitment period for brown shrimp postlarvae is February and March; for white shrimp it is June through September (Williams 1965).

Because osmoregulation is impaired at low temperatures, we considered that low salinity could increase mortality caused by low temperatures. Although salinity records were not available, we compared local rainfall measurements with pink shrimp landings from 1962 to 1981.

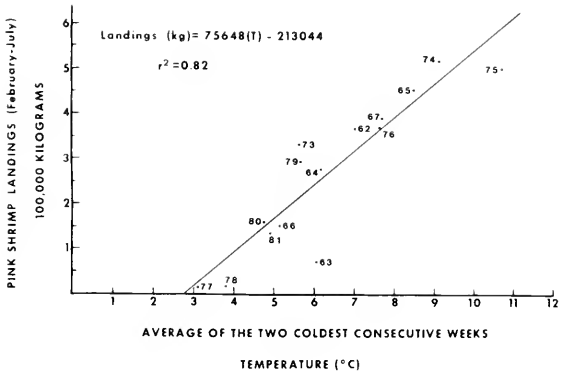

FIGURE 4.—Relation of pink shrimp landings in North Carolina to the average water temperature of the two coldest consecutive weeks in the Newport River estuary. Numbers by dots represent year of landings. (Actual landings of 198,000 kg were predicted to be 165,200 kg, based on the coldest average biweekly period temperature in 1982 of 5.0°C.)

We found no correlation between rainfall and landings ($r^2 = 0.003$) (Table 1). Further, rainfall added no significant contribution to the explanation of variance in landings data when it was included with temperature as a predictive variable (multiple $R^2 = 0.826$). Both the driest (18.0 cm in 1965) and wettest (49.3 cm in 1974) winters occurred in years when landings were very large, approximately 500 metric tons. Williams (1969a) also found no significant relationship between rainfall and total catch of all shrimp species. However, Hunt et al.[3] reported that salinities ≥10‰ and temperatures ≥20°C during April and May are necessary for good brown shrimp harvests in North Carolina. Similarly, Gunter and Hildebrand (1954) found a strong correlation of total rainfall and white shrimp catch in Texas.

Deviations from the shrimp landings-temperature relationship may, in part, be due to the process of estimating landings. Errors may include improper species identification by fish dealers, lack of accuracy in estimated weight landed, and incomplete landing coverage. The direct trading of shrimp to private individuals by numerous part-time fishermen, plus the recreational landings, neither of which is reported, undoubtedly causes an underestimate of total

[3]Hunt, J. H., R. J. Carroll, V. Chinchilli, and D. Frankenberg. 1980. Relationship between environmental factors and brown shrimp production in Pamlico Sound, North Carolina. N.C. Dep. Nat. Resour. Community Dev. Div. Mar. Fish. Spec. Sci. Rep. 33, 29 p.

landings (Caillouet and Koi 1980). On the other hand, because of increased demand and higher prices for shrimp, fishing effort is probably more intensive in recent years. We did not consider effort in our analysis because reliable data were not available. Williams (1969b) concluded that pounds landed almost paralleled his calculated catch-effort index and therefore that actual harvest data satisfactorily represented annual productivity independent of effort. Another source of variability to be considered, the annual variation in the recruitment of postlarvae, was dismissed because Williams (1969b) and Williams and Deubler (1968) found no relation between densities of penaeid shrimp postlarvae and subsequent landings. Similarly Lindner and Anderson (1956) found that a severe cold kill of adult white shrimp in 1940 had no effect on the next year's landings.

A number of complications in relating catch and climate were listed by Austin and Ingham (1979). In our study, which began with a conceptual model of an organism and its relation to a physical parameter, some of the following suggested complications were mitigated: 1) A causal relationship of temperature to production was biologically appropriate, because the life history and temperature tolerance of pink shrimp are known; 2) the use of proxy data (air temperature instead of water temperature) was avoided; 3) major variations in the shrimp landings are probably due to cold kill of overwintering shrimp caused by cold-water temperatures ($r^2 = 0.82$); 4) while the quality of the biological data (landings) cannot be judged, the length of the time series (15 yr) is probably adequate; 5) an interest does exist among fishery biologists and managers in using environmental data and relationships for predictive, explanatory, or modeling purposes; 6) although environmental data were point source, landings were from a geographical area (<100 km radius) sufficiently restricted so as not to have masked biota-environmental relations.

ACKNOWLEDGMENTS

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SEASONAL ABUNDANCE, COMPOSITION, AND PRODUCTIVITY OF THE LITTORAL FISH ASSEMBLAGE IN UPPER NEWPORT BAY, CALIFORNIA

LARRY G. ALLEN[1]

ABSTRACT

This study was designed to characterize the littoral fish populations by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) important environmental factors.

Monthly samples (January 1978 to January 1979) obtained with four quantitative sampling methods at three stations in upper Newport Bay yielded 55,561 fishes from 32 species which weighed 103.5 kg. The top five species made up over 98% of the total number of individuals. One species, *Atherinops affinis*, predominated in numbers (76.7% of all fishes) and biomass (79.8%). This dominance was reflected in the low overall H' diversity values for numbers ($H'_N = 0.89$) and biomass ($H'_B = 0.84$). Number of species, number of individuals, and biomass were greatest during the spring and summer.

Quantitative clustering of species based on individual samples revealed five species groups which reflected both microhabitat and seasonal differences in the littoral ichthyofauna. Species Group I was made up of five resident species—*A. affinis*, *Fundulus parvipinnis*, *Clevelandia ios*, *Gillichthys mirabilis*, and *Gambusia affinis*. Species Groups II-VI were composed of summer and winter periodics and rare species.

The mean annual production (9.35 g dry weight/m^2 determined by the Ricker production model) of the littoral zone fishes was among the highest of reported values for comparable studies. This high annual production was mainly the result of the rapid growth of large numbers of juveniles that utilized the littoral zone as a nursery ground. Young-of-the-year *Atherinops affinis* contributed 85% of this total production.

Canonical correlation analysis indicated that temperature and salinity together may influence littoral fish abundance. These two abiotic factors accounted for 83% of the variation in the abundances of individual species. Emigration from the littoral zone, therefore, seems to be cued by seasonal fluctuations in temperature and salinity. I propose that this offshore movement forms an important energy link between the highly productive littoral zone and local, nearshore marine environment.

Semienclosed bays and estuaries are among the most productive areas on Earth, ranking with oceanic regions of upwelling, African savannas, coral reefs, and kelp beds (Haedrich and Hall 1976) in terms of animal tissue produced per year. Bays and estuaries harbor large stocks of nearshore fishes and are important feeding and nursery grounds for many species of fish, including commercially important ones. However, the high productivity of fishes is accompanied by low diversity (Allen and Horn 1975) which probably reflects the stressful ecological conditions in bays and estuaries and the high physiological cost of adaptation to them (Haedrich and Hall 1976). The few studies that have dealt with productivity in estuarine fishes were summarized by Wiley et al. (1972) and Adams (1976b).

Utilization of temperate embayments by juvenile and adult fishes is markedly seasonal with high abundances corresponding to the warmer, highly productive months of spring through autumn. Seasonal species typically spend one spring-autumn period in the shallows of a bay growing at an accelerated rate in the warm, highly productive waters (Cronin and Mansueti 1971).

Most studies to date dealing with composition and temporal changes of bay-estuarine fish populations have been conducted on the Gulf of Mexico and Atlantic coasts of the United States where estuaries are larger and more numerous than those on the Pacific coast (e.g., Bechtel and Copeland 1970; Dahlberg and Odum 1970; Derickson and Price 1973; McErlean et al. 1973; Oviatt and Nixon 1973; Recksiek and McCleave

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1973; Haedrich and Haedrich 1974; Targett and McCleave 1974; Livingston 1976; Moore 1978; Shenker and Dean 1979; Orth and Heck 1980). Although quantitative in nature, many of these investigations suffer from the inefficient (Kjelson and Johnson 1978) trawl sampling gear used and the high mobility of most fishes. Adams (1976a, b) used dropnet samples to accurately assess the density and productivity of the fishes of two North Carolina eelgrass beds. Weinstein et al. (1980) used a combination of block nets, seines, and rotenone collections to derive accurate quantitative estimates of fishes in shallow marsh habitats in the Cape Fear River Estuary, N.C.

Previous investigations of fishes in Newport Bay have included a species list (Frey et al. 1970), a general species account (Bane 1968), two individual species accounts (Fronk 1969; Bane and Robinson 1970), and two studies on the population ecology of the fauna based on juveniles and adults (Posejpal 1969; Allen 1976). An assessment of the ichthyoplankton and demersal fish populations during 1974-75 (Allen and White in press) is the most comprehensive work to date.

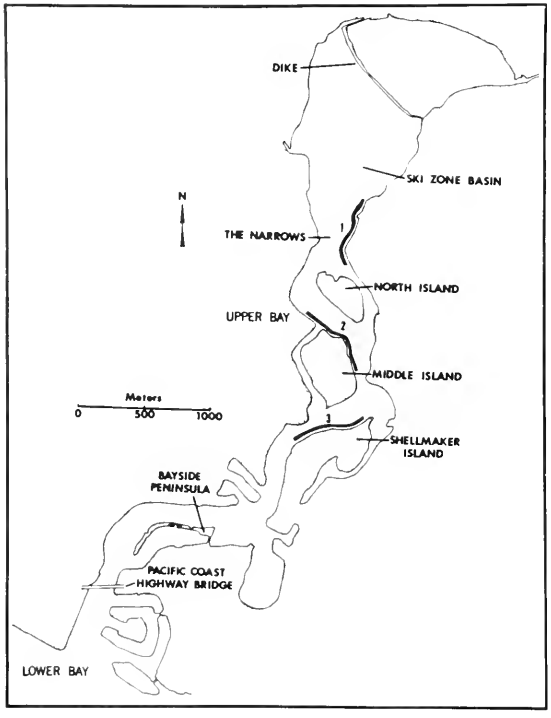

FIGURE 1.—Map of upper Newport Bay, Orange County, Calif., with the locations of the three sampling stations.

Despite these studies, a substantial component of the ichthyofauna, the littoral fishes of the upper bay (0-2 m depth from mean higher high water), had not been adequately sampled. In a study of the demersal ichthyofauna of Newport Bay during 1974-75 (Allen 1976), I found that three—*Atherinops affinis*, *Fundulus parvipinnis*, and *Cymatogaster aggregata*—of the five most numerous species were the ones that occurred in the shallow water over the mudflats which cover about 60-70% of the surface area of the upper bay reserve. Despite their high numerical ranking, the relative abundances of these littoral species were underestimated because sampling was carried out almost exclusively by otter trawls in the deeper channels of the upper bay. The recognition of this gap in our knowledge served as the impetus for the present study.

The main purposes of this study were to characterize the littoral ichthyofauna of upper Newport Bay quantitatively by 1) composition and principal species, 2) diversity and seasonal dynamics, 3) productivity, and 4) key environmental factors that are influencing this fish assemblage.

METHODS AND MATERIALS

Study Area

Newport Bay (lat. 33°37′30″N, long. 117° 54′ 20″W) is located in Orange County, Calif., 56 km southeast of Los Angeles and 140 km north of the Mexican border (Fig. 1). The upper portion is the only large, relatively unaltered bay-estuarine habitat in California south of Morro Bay (lat. 34.5°N). The low to moderately polluted lower portion, commonly called Newport Harbor, has been severely altered by dredging activities, landfills, and bulkheads to accommodate more than 9,000 boats. The study area, the upper two-thirds of the upper bay, is bordered almost completely by marsh vegetation and mudflats. The California Department of Fish and Game purchased and set aside this area as an ecological reserve in 1975.

Three stations, about 0.5 km in length, were spaced evenly along the shore of the upper Newport Bay (Fig. 1). Sampling was stratified based on prior information on the uniqueness of the fish fauna of the three areas (Allen 1976). This design also allowed thorough coverage of the study area. Each station was situated on a littoral (intertidal) mudflat area adjacent to marsh vegetation

and was divided into 10 numbered sections of equal size. Selection of the section sampled each month was random in order to satisfy statistical assumptions and minimize the impact of sampling on any particular section from month to month. Each station included a tidal creek or pool (panne) which was sampled on the marsh islands.

Sampling Procedures

Monthly samples were taken at the three stations during the 13-mo period from January 1978 to January 1979 for a total of 39 station samples. Sampling was carried out within ±3 h of daytime neap high tide to minimize tidal level effects. Two days were usually required to sample three stations, stations 1 and 2 the first day and station 3 the second.

Four types of sampling gear were employed at each station as follows:

1) A 15.2 m × 1.8 m bag seine (BS) with 6.4 mm mesh in the wings and 3.2 mm mesh in the 1.8 × 1.8 × 1.8 m bag was used twice at each station. Hauls were made by setting the net parallel to and 15 m off the shore at a depth of 1-2 m. The BS was then hauled to shore using 15 m polypropylene lines attached to 1.8 m brails on each end of the net. Each haul sampled an area of 220 m^2.

2) A 4.6 m × 1.2 m small seine (SS) with 3.2 mm mesh was pulled 10 m along and 2 m from the shore (at a depth to 1 m) and pivoted to shore. Two hauls were made in the inshore area and one haul in the panne at each station. Each haul sampled an area of 62.4 m^2. [One exception to the sampling routine occurred at station 3 panne in April 1978 when no sample was taken due to a dry panne.]

3) A 2.45 × 2.45 × 1.0 m dropnet (DN) with 3.2 mm mesh was used to sample the water column and bottom at 0.5-1.5 m depth. The DN was suspended from a 5.0 × 5.0 × 1.0 m aluminum pipe frame, released by pins at each corner. Two 19 l plastic buckets were attached to each corner of the frame for flotation. The net and frame were maneuvered into position, anchored, and left undisturbed for 10 min. After release the DN was pursed by the chain line and hauled to shore by nylon line. The DN sampled an area of 6.0 m^2.

4) A small, square enclosure (SE) was used in conjunction with an anesthetic (quinaldine mixed 1:5 with isopropyl alcohol) with the intent of sampling small burrow inhabiting fishes, especially gobies. The SE was constructed of heavy duck material mounted on a 1.0 × 1.0 × 1.0 m collapsible frame of 25.0 mm PVC pipe and sampled 1.0 m^2 of bottom. The SE was set at three randomly chosen positions in an undisturbed portion of each station section at a depth of 0.5-1.0 m. The bottom of the SE was forced into the upper few centimeters of substrate and the quinaldine mixture added to the enclosed water column. The enclosed volume and shallow substrate was then thoroughly searched for 10 min using a long-handled dip net of 1.0 mm mesh.

A detailed comparison of the effectiveness of these four methods is the subject of a separate paper (Horn and Allen[2]).

Ten samples were taken at each of the three stations each month (2 BS samples, 3 SS samples, 2 DN samples, 3 SE samples) for a total of 30 samples/mo and 289 samples over the study (minus one SS haul in April 1978 at station 3).

Catches were either frozen on Dry Ice[3] or preserved in 10% buffered Formalin. Specimens >150 mm SL were injected abdominally with 10% buffered Formalin. Subsamples of frozen specimens were oven dried (40°C) for 48-72 h for dry weight determination. Mean dry weights were based on a minimum of 20 individuals/size-class of each common species at each station each month.

Data on six abiotic factors were recorded or determined for each station: temperature, salinity, dissolved oxygen, sediment particle size, depth of capture (by individual samples), and distance into the upper Newport Bay from the Highway 1 bridge (see Fig. 1).

Production Estimation

Production is the total amount of tissue produced during any given time interval including that of individuals which do not survive to the end of that time interval (Ivlev 1966). Productivity is the rate of production of biomass per unit of time (Wiley et al. 1972). Production of a fish stock

[2]Horn, M. H., and L. G. Allen. Comparison of methods for sampling shallow-water estuarine fish populations. Manuscr. in prep. California State University, Fullerton, Fullerton, CA 92634.

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

is the product of the density of fish and the growth of the individuals (Ricker 1946).

An HP9100A program was developed with the aid of Joel Weintraub (California State University, Fullerton) to calculate the production of each recognizable size-class of the common species, those which were collected in at least 2 consecutive months at each station. The model used was that proposed by Ricker (1946) and modified by Allen (1950) and is calculated as follows:

$$P = G\bar{B}$$

where $G = \dfrac{\log_e \bar{w}_2 - \log_e \bar{w}_1}{\Delta t}$ is the instantaneous coefficient of growth;

$$\bar{B} = \frac{B_1(e^{G-Z}-1)}{G-Z}$$ is the average biomass over the time interval;

$$Z = \frac{-(\log_e N_2 - \log_e N_1)}{\Delta t}$$ is the instantaneous coefficient of population change of the immediate sampling area (station) attributable to mortality and migration;

B is the biomass density of fishes at t_1; w_1, w_2 are the mean weights of individuals at time t_1 and t_2; and N_1, N_2 are the numbers of fishes present at t_1 and t_2. $G-Z$ is the net rate of increase in biomass during Δt (1 mo).

The model assumes that production data need not be corrected for immigration and emigration of fishes in and out of the sampling area, provided the density and growth by size-class are estimated frequently enough to accurately assess the abundance and growth of fishes actually in the sampling area (Chapman 1968).

In the present study, growth increments were estimated from length-frequency data for fishes from all three stations each month for each size-class. The length data, therefore, were representative of the entire population of the size-class in the upper Newport Bay and served to minimize the effects which localized movements into and out of a particular station have on monthly growth values. The average weight, $\bar{w}$, of a size-class per month was calculated as follows: 1) Dry weight equivalent for the median length in a size interval (5 mm intervals) was determined using standard length to dry weight curves for each common species; 2) the proportion (range 0-1) of individuals represented in the size interval was multiplied by the dry weight equivalent for the interval; 3) the products were then summed for all size intervals contained within the particular size-class of the species yielding an average weight, $\bar{w}$. This method proved to be more accurate than simply taking the mean length of the entire size-class and determining the dry weight equivalent.

The "best estimate" of biomass density (B) for each discernible size-class was determined in the following manner: 1) The biomass density (wet weight) derived from the method (BS, SS, DN, or SE) shown to be most effective at sampling the particular species was used. Table 1 lists the species with corresponding collecting gear ranked by their effectiveness at capturing the species. This list is based on a comparative study of the sampling methods (Horn and Allen footnote 2); 2) if, as in a few cases, the biomass estimated was inordinately high, due to a large catch in one replicate sample, the estimate defaulted to the next gear type in the rank order; 3) the biomass estimate in wet weight was converted to a dry weight (DW) equivalent by a conversion factor determined for each species and entered into the production model as B_1 (g DW/m^2). Production is the total of all positive values for size-classes during a time period (1 mo in this case) at each station. Negative values were due to sampling error and emigration and were not included in production estimates.

Large individuals (>100 mm SL) of *Mugil cephalus* were not included in production esti-

TABLE 1.—Methods for best estimate of species densities ranked by effectiveness (Horn and Allen text footnote 2). BS = bag seine; SS = small seine; DN = dropnet; SE = square enclosure.

Species	Methods ranked by effectiveness
Atherinops affinis	BS, SS
Fundulus parvipinnis	SS, BS
Clevelandia ios	SE, SS, DN
Anchoa compressa	BS, SS, DN
Gambusia affinis	SS, BS
Cymatogaster aggregata	BS, DN, SS
Gillichthys mirabilis	SS, SE, BS
Anchoa delicatissima	BS, SS
Mugil cephalus	SS, BS
Engraulis mordax	BS, SS
Leuresthes tenuis	BS, SS
Quietula ycauda	DN, SS
Ilypnus gilberti	DN, SS
Syngnathus spp.	SS, DN
Hypsopsetta guttulata	SS, DN
Lepomis macrochirus	BS, SS
Lepomis cyanellus	BS, SS
All other species	BS, SS

mates because quantitative estimates of densities could not be obtained for the large members of this mobile species.

Data Analysis

Cumulative Species Curve

The cumulative number of species in February (low fish density) and June (high fish density) was plotted against the number of samples taken in order to assess the adequacy of sampling. Two random sequences were used for the arrangement of the 30 samples taken each month by the four methods. Each method sampled a unique subhabitat within the littoral zone. Cumulative species curves (reflecting presence/absence) were based on a combination of methods to insure that all possible species occupying the littoral zone at a particular time were represented.

Diversity

Both the Shannon-Wiener information function (Shannon and Weaver 1949) and species richness were used as measures of diversity for pooled station and upper bay samples. The Shannon-Wiener index reflects both species richness and evenness in a sample.

Cluster Analysis and Canonical Correlation

The Ecological Analysis Package (EAP) developed by R. W. Smith was used at the University of Southern California Computer Center to determine species associations (cluster analysis), species abundance correlations to abiotic factors (multiple regression subprogram), and possible effects of abiotic factors on individual species abundance (canonical correlation).

The cluster analysis utilized the Bray-Curtis index of dissimilarity (Clifford and Stephenson 1975). This index allowed quantitative clustering without assuming normality in the sampled population. A square-root transformation of species counts was done to counter the tendency of this index to overemphasize dominant species.

Canonical correlation analysis was used to determine whether and to what extent abiotic factors interacted with individual species abundances in the 39 station samples over the study period. Two separate canonical correlation analyses were made: The first run included six abiotic factors—temperature (TEMP), salinity (SAL), dissolved oxygen (DO), distance into the upper bay from the Highway 1 bridge (DSTUPB), average particle size of the sediment (APRTSZ), and depth of capture (DPTHCAP); the second included only temperature and salinity to determine the amount of variation these two factors accounted for alone.

RESULTS

Temperature and Salinity Patterns

Water temperatures of the littoral zone at all three stations increased steadily during the period January-June from 14°-15°C to 26°-28°C (Fig. 2). The temperatures remained high (>25°C) throughout the summer months and then declined gradually until November. Between November and December the temperature dropped sharply at each station. Temperatures in the pannes were generally higher than the tempera-

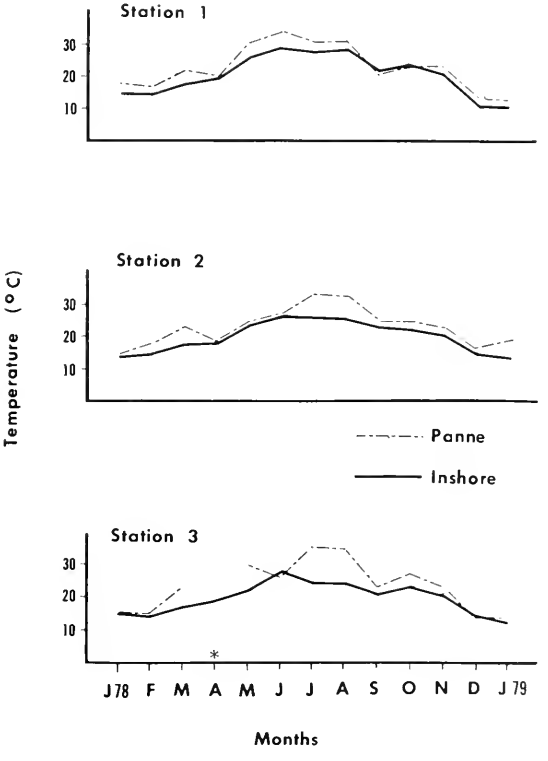

FIGURE 2.—Month-to-month variation (January 1978-January 1979) in water temperature (°C) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

tures along the shore especially in the summer months (July-September).

Salinity varied more than temperature (Fig. 3) due to rainfall and periodic runoff from surrounding urban areas. In general all stations had low salinities during January through March 1978, a period of heavy rainfall. After May 1978, salinities remained high (between 25 and 32 ppt) with decreases in June 1978 (stations 1 and 3, unknown cause), September 1978 (all stations due to heavy rainfall), and January 1979 (station 3 due to rainfall). Panne salinities at station 1 were consistently low (usually <6 ppt) indicating a constant freshwater input. The pannes at stations 2 and 3, however, usually had salinities equal to or higher than the alongshore area due to evaporation.

Total Catch

Sampling during the 13-mo period yielded 55,561 individuals of 32 species that weighed a total of 103.5 kg (Table 2).

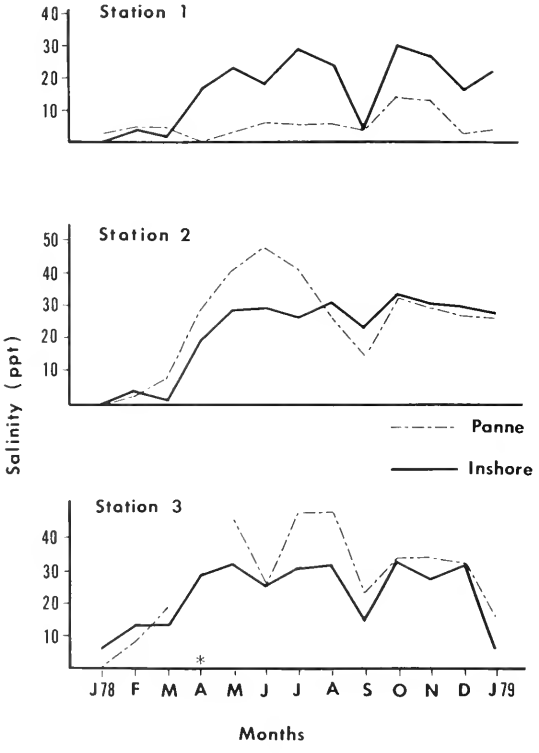

FIGURE 3.—Month-to-month variation (January 1978-January 1979) in salinity (ppt) for the alongshore area and panne at each of the three sampling stations. (* = panne dried-up.)

Atherinops affinis greatly predominated in numbers (76.7%) and biomass (79.9%). *Fundulus parvipinnis* ranked second in both numbers (12.1%) and biomass (7.6%), followed in order by *Gambusia affinis* (5.5% numbers), *Clevelandia ios* (2.4% numbers), and *Anchoa compressa* (1.2% numbers). These five species accounted for 98% of the total number of individuals and 96% of the total biomass (Table 2). The skewed distribution of number of individuals among species was reflected in the relatively low overall H' diversity values of 0.89 for numbers (H'_N) and 0.84 for biomass (H'_B). The vast majority of individuals of most species were either young-of-the-year or juveniles.

Station 1—A total of 13,859 individuals representing 19 species was collected during the year. The catch totaled 22.7 kg. All three of these totals were the lowest of those from the three stations. Overall H' diversity for numbers was 1.17 and for biomass, 0.89. *Atherinops affinis* ranked first in numbers (55.2%) and biomass (76.7%) but was less abundant here than at stations 2 and 3. *Gambusia affinis* (20.6%) and *Fundulus parvipinnis* (19.1%) were common at this station especially in the panne.

Station 2—The greatest number of individuals (24,813) and biomass (42.9 kg) were collected at this site. Although 27 species were captured, over 90% of these individuals were from one species, *Atherinops affinis*. The large number of attached eggs and small (<20 mm) fish caught in July (52% of all *A. affinis*) indicated that this area was a breeding site for *A. affinis*. *Fundulus parvipinnis* (4.4%) was second in numerical rank. H' for numbers (0.49) and biomass (0.70) were low.

Station 3—A total of 16,889 fishes belonging to 23 species were obtained at this station. *Atherinops affinis* made up 74.4% of the individuals and 78.8% of the 37.9 kg total biomass. Other important species in order of decreasing numerical abundance were *Fundulus parvipinnis* (17.6%), *Clevelandia ios* (3.4%), *Cymatogaster aggregata* (1.3%), and *Anchoa compressa* (1.3%). Overall, H'_N and H'_B were 0.87 and 0.85, respectively.

Cumulative Species Curves

Cumulative species curves from February and June (Fig. 4) reached an asymptote before 20 samples (about 66% of total samples), indicating

TABLE 2.—Monthly abundance and biomass for fish species inhabiting the littoral zone of upper Newport Bay totaled for stations 1-3 (January 1978-January 1979).

Species	January 1978		February		March		April		May		June		July	
	No	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No	Wt (g)	No	Wt (g)	No.	Wt (g)
Atherinops affinis	15	70.5	5	158.3	4	92.0	15	59.1	322	1,212.1	6,296	2,377.6	19,817	19,093.3
Fundulus parvipinnis	377	315.7	208	198.3	181	90.4	17	20.7	35	92.2	89	112.3	758	854.8
Gambusia affinis	46	10.3	23	7.1	9	3.2	5	2.8	56	7.1	235	107.4	573	342.9
Clevelandia ios	49	21.4	39	14.3	80	12.9	47	6.1	100	22.4	74	15.8	485	109.0
Anchoa compressa	26	82.9	1	1.2	15	29.4	136	629.3	317	4,393.4	98	1,154.6	77	920.5
Cymatogaster aggregata							11	11.5	141	196.8	4	5.7		
Gillichthys mirabilis	12	2.4	38	5.9	14	3.5	5	10.0	17	39.6	49	127.1	52	141.4
Anchoa delicatissima	10	6.5	1	0.2	28	16.8	47	86.7	17	48.2			1	3.0
Mugil cephalus	41	78.0	11	7.1	1	1.5	1	555.5	1	550.0				
Engraulis mordax													81	89.4
Leuresthes tenuis														
Quietula ycauda	1	1.0							3	1.4	9	3.9	28	14.9
Ilypnus gilberti									3	0.5	10	1.0	24	6.5
Lepomis cyanellus			1	5.2										
Syngnathus auliscus									4	3.6	10	8.7	4	3.3
Hypsopsetta guttulata									10	1.9	4	12.9	2	18.2
Lepomis macrochirus	2	8.1	4	22.2	2	4.1								
Syngnathus leptorhynchus							1	2.1			2	2.6		
Leptocottus armatus					1	1.0			2	4.7	1	1.6		
Acanthogobius flavimanus							2	0.5	1	4.0				
Paralichthys californicus													2	5.4
Pimephales promelas			2	0.2										
Morone saxatilis											1	317.1		
Urolophus halleri														
Mustelus californicus													1	58.0
Seriphus politus														
Cynoscion nobilis													1	6.6
Sphyraena argentea														
Girella nigricans													1	0.4
Symphurus atricauda			1	0.2										
Porichthys myriaster														
Umbrina roncador														
Totals	579	596.8	334	420.2	335	254.8	287	1,384.3	1,029	6,577.9	6,882	4,248.3	21,907	21,667.6
n	10		12		10		11		15		14		16	
H'	1.29	1.46	1.33	1.27	1.37	1.55	1.61	1.22	1.76	1.07	0.44	1.24	0.46	0.56

TABLE 2.—*Continued.*

Species	August		September		October		November		December		January 1979		Totals			
	No.	Wt (g)	No	Wt (g)	No.	Wt (g)	No.	Wt (g)	No.	Wt (g)	No	Wt (g)	No.	% No.	Wt (g)	% Wt
Atherinops affinis	4,645	13,181.2	4,122	9,606.2	2,902	14,016.0	2,474	12,409.8	1,143	5,738 8	831	4,650.1	42,591	76.67	82,665.0	79.86
Fundulus parvipinnis	312	250.1	1,707	2,323.0	1,023	2,638.8	1,356	738.0	593	259 7	66	26.5	6,722	12.10	7,920.5	7 65
Gambusia affinis	252	42 4	1,029	399.4	680	126.2	149	15.2	20	2.1			3,077	5.54	1,066.1	1.03
Clevelandia ios	68	16.4	151	41.8	66	16.3	142	31.3	28	3 9	5	1.1	1,334	2.40	312.7	0.30
Anchoa compressa	7	104.9	3	53.1	4	104 8							684	1.23	7,474 1	7.22
Cymatogaster aggregata	61	390.9	2	16.6			2	34 1	1	22 6	1	12.4	223	0.40	690 6	0.67
Gillichthys mirabilis	4	27.0	1	20.0	4	37 1	1	12.0			6	0.3	203	0.37	426.3	0.41
Anchoa delicatissima	64	234 4	26	71.7	1	3.5							195	0.35	471.0	0.46
Mugil cephalus									68	13.3	9	1.5	132	0.24	1,206.9	1.17
Engraulis mordax			29	58.6	2	7 2					1	—	113	0.20	155.2	0.15
Leuresthes tenuis	85	57.8	3	2.3									88	0.16	60 1	0.06
Quietula ycauda	5	1.9	4	1.5	2	0 4	1	0.1					53	0.10	25.1	0.02
Ilypnus gilberti							1	0.1					38	0.07	8.1	0.01
Lepomis cyanellus			31	49.3									32	0.06	54.5	0.05
Syngnathus auliscus	1	0.4			1	0 1							20	0.04	16.1	0.02
Hypsopsetta guttulata							1	2.9			2	0.2	19	0.03	36.1	0.03
Lepomis macrochirus													8	0.01	34.4	0.03
Syngnathus leptorhynchus	1	2.8	3	5.2							1	0.3	8	0.01	13.0	0.01
Leptocottus armatus													4	0.01	7.3	0.01
Acanthogobius flavimanus													3	0.01	4.5	<0.01
Paralichthys californicus													2	<0.01	5.4	0.01
Pimephales promelas													2	<0.01	0.2	<0.01
Morone saxatilis													1	<0.01	317.1	0.31
Urolophus halleri	1	430 0											1	<0.01	430.0	0.42
Mustelus californicus													1	<0.01	58.0	0.06
Seriphus politus					1	0.3							1	<0.01	0.3	<0.01
Cynoscion nobilis													1	<0.01	6 6	0.01
Sphyraena argentea							1	4 2					1	<0.01	4 2	<0.01
Girella nigricans													1	<0.01	0.4	<0.01
Symphurus atricauda													1	<0.01	0.2	<0.01
Porichthys myriaster							1	0.1					1	<0.01	0.1	<0.01
Umbrina roncador	1	44 2											1	<0.01	44.2	0.04
Totals	5,507	14,784 4	7,111	12,648.7	4,686	16,950.7	4,129	13,247.8	1,853	6,040 4	922	4,692.4	55,561		103,514.3	
n	14		13		11		11		6		9		32			
H'	0.69	0.55	1 10	0.77	0.99	0.54	0 92	0.27	0.90	0.23	0.42	0.06	0.89		0.84	

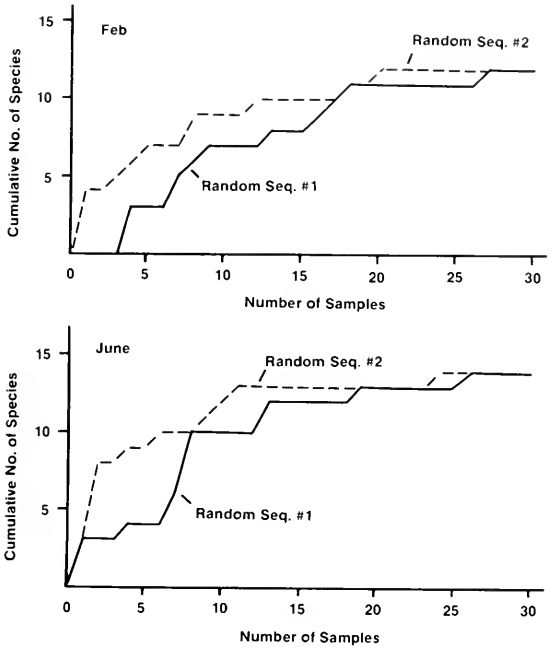

FIGURE 4.—Cumulative number of species as a function of the number of samples of all methods at stations 1-3 combined in upper Newport Bay for two different months (February and June 1978) during the study period. Curves were generated by two random sequences for each month.

that the range of fish species in the area had been adequately sampled by the four methods. Accumulation of species in June, however, was generally more rapid than in February.

Seasonal Abundance and Diversity

Fish abundance and diversity fluctuated markedly during the 13 mo of the study (Fig. 5). As a whole, the ichthyofauna of the littoral zone showed increased species richness from 10 species in January to 16 species in July 1978. The number of species was elevated (>14) for the entire spring-summer period from May to August 1978. Richness then decreased through the fall, reaching its lowest point of six species in December 1978. Diversity H' values fluctuated in a pattern opposite to that of species richness. H'_N decreased during the summer from a high in May of 1.76 to a low in June of 0.44. H'_B also decreased sharply in summer but unlike H'_N continued to decline for the remainder of the study. Both the number of individuals and biomass began to increase dramatically during May 1978 and reached peaks of 21,907 individuals and 21.7 kg in June. Both numbers and biomass decreased in August with number of individuals increasing again in September. Biomass declined once again in September during a period of rainfall and then increased in October. In the months from October 1978 to January 1979 a rapid decline in both numbers and biomass was evident and was especially pronounced from November to December. A greater number of individuals (992-579) and much greater biomass (4,692-597 g) was obtained in January 1979 than in January 1978.

Species Associations

Cluster analysis based on individual samples yielded five species groups which, upon further

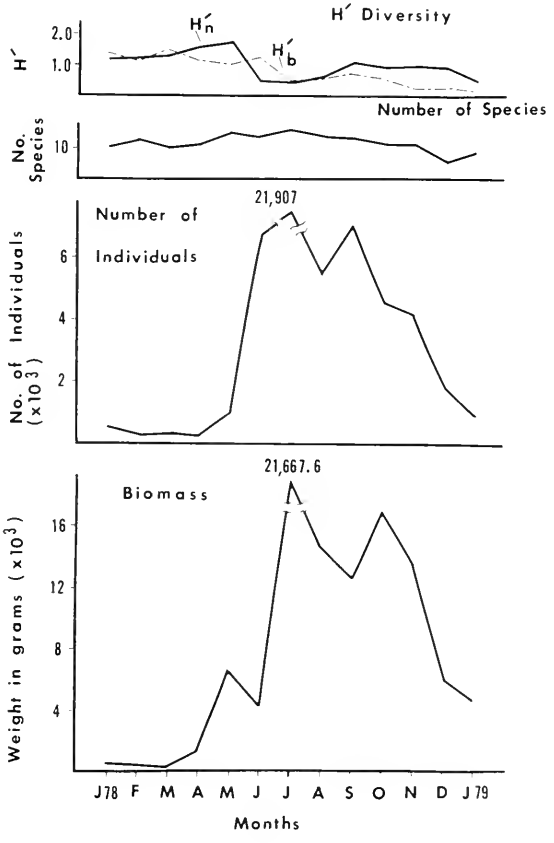

FIGURE 5.—Monthly variation (January 1978-January 1979) in total number of species, diversity H′ (for numbers, H'_N, and biomass, H'_B), number of individuals and biomass (g) for fishes collected by all methods at stations 1-3 combined in the littoral zone of upper Newport Bay.

examination, reflected both spatial (microhabitat) and seasonal differences in the littoral ichthyofauna (Fig. 6).

Group I was a loosely associated group of the five resident species (maintain populations year round in littoral zone) which could be further divided into three subgroups. Subgroup A had only one member, *Atherinops affinis*, an abundant schooling species. *Clevelandia ios* and *Gillichthys mirabilis* which comprised subgroup B are burrow-inhabiting gobiids of the shallows and pannes. Subgroup C included two species, *Fundulus parvipinnis* and *Gambusia affinis*, which inhabited pannes and other high intertidal areas. *Clevelandia ios*, *G. mirabilis*, and *F. parvipinnis* are residents of salt marshes in California and other west coast estuaries and are probably the species most threatened by alterations of these habitats.

Group II consisted of three midwater schooling species—*Anchoa compressa*, *A. delicatissima*, and *Cymatogaster aggregata*—most of which were caught mainly from January to August.

Group III was made up of three distinctly seasonal, benthic species: Two gobiids, *Quietula ycauda* and *Ilypnus gilberti*, and a cottid, *Leptocottus armatus*, which was relatively rare during 1978 compared with previous years (pers. obs.).

Group IV included an engraulid, *Engraulis mordax*; syngnathids, Syngnathus spp. (including *S. auliscus* and *S. leptorhynchus*); and the pleuronectid, *Hypsopsetta guttulata*. These species were seasonally present in mid- to late summer. Members of this group were only loosely associated (> 80% distance).

Group V was composed of four species which were collected at times of low salinities. *Lepomis macrochirus* and juveniles of *Mugil cephalus* were sampled together early in the year (January-March 1978). *Lepomis cyanellus* and *Leuresthes tenuis* were found together only in September.

Group VI included 12 rare species, most of which could be considered summer periodics in the littoral zone in 1978. These were *Umbrina roncador*, *Urolophus halleri*, *Paralichthys californicus*, *Mustelus californicus*, *Cynoscion nobilis*, *Acanthogobius flavimanus*, *Sphyraena argentea*, *Girella nigricans*, *Symphurus atricauda*, *Porichthys myriaster*, *Morone saxatilis*, and *Seriphus politus*.

Members of the species groups identified in the dendrogram (Fig. 6) are illustrated in dia-

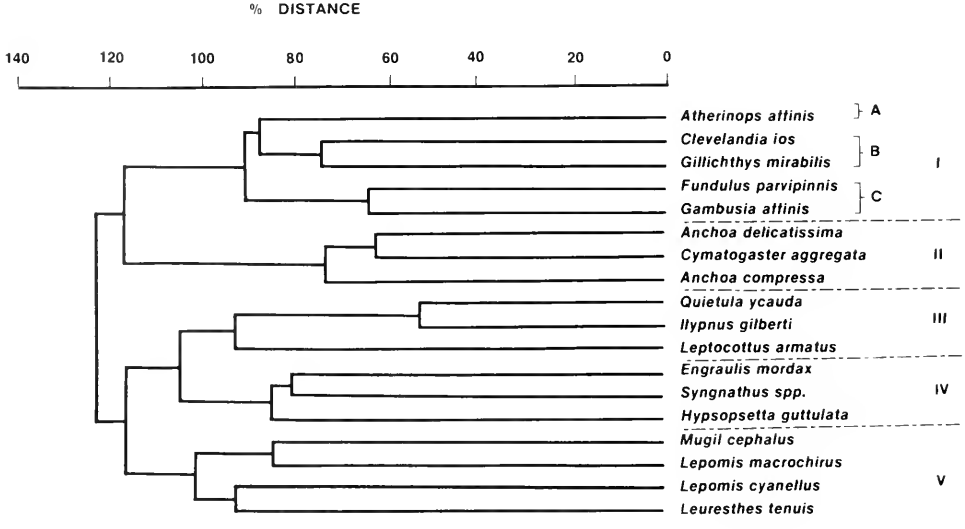

FIGURE 6.—Dendrogram of the clustering of littoral fish species by individual samples taken at stations 1-3 in upper Newport Bay, five species groups (Roman numerals) are recognized according to the Bray-Curtis index of dissimilarity (% distance). A, B, and C are subgroups of species Group I.

grams (Figs. 7-9), depicting occurrences in the alongshore area or panne during three different time periods (January-March 1978, April-September 1978, and October 1978-January 1979). Only species with ≥5 individuals during each time segment were included in the diagrams. These diagrams illustrate the high degree of seasonality within this fish assemblage.

During the January-March 1978 period of heavy rainfall, members of three species groups (I, II, and V) were present in relatively low abundances (Fig. 7). A halocline existed at station 3 during this period, and *Atherinops affinis* was collected only seaward of the halocline at this station. Representatives of group V, *Mugil cephalus* juveniles and *Lepomis macrochirus*, were found associated with very low salinities. Large *M. cephalus* were observed in both the channel and littoral areas during most of the year.

The spring-summer period of April-September 1978 was characterized by increased water temperatures and salinities, accompanied by increased numbers of species and individual fishes (Fig. 8). Green algal beds, composed primarily of *Enteromorpha* sp., *Chaetomorpha linum*, and *Ulva lobata*, developed along the shore of the entire upper bay, and served as a nursery area for large numbers of juvenile fishes. All species groups, except V, were represented during this time. Juveniles of *Atherinops affinis* occurred in large numbers in the shallows with juvenile *Cymatogaster aggregata* also being abundant at station 3. Young-of-the-year *F. parvipinnis* were very abundant in the pannes, especially at stations 1 and 3.

By October the extensive algal beds had disappeared. The October 1978-January 1979 period was marked by decreased number of species and abundance (Fig. 9). The only common species were members of group I (residents) with a few juvenile *M. cephalus* representing group V.

Productivity

Annual production (mean of three stations by month) of the entire upper Newport Bay was 9.35 g DW/m^2 per year (Table 3). Young-of-the-year *Atherinops affinis* contributed 85.1% to total production followed by *Anchoa compressa* (4.9%) and *Fundulus parvipinnis* (4.2%).

Productivity was highly seasonal with the spring-summer period (April-September) accounting for 75.9% of the total annual production (Table 3, Fig. 10). Productivity, which was very

TABLE 3.—Monthly mean production (g DW m^{-2}) for individual species inhabiting the littoral zone (excluding panne) of upper Newport Bay (February 1978-January 1979).

Species	Feb	Mar	Apr.	May	June	July	Aug.	Sept.	Oct	Nov	Dec.	Jan.	Total annual	% total production
Atherinops affinis (adult)				0.0280	0.1049								0.1329	1.42
A. affinis (78 class)					0.0800	0.6764	5.1397		1.2942	0.6428		0.1307	7.9638	85.15
Fundulus parvipinnis	0.0005		0.0007	0.0240	0.0167	0.1323	0.0352	0.0826	0.1033				0.3953	4.23
Clevelandia ios	0.0003			0.0027	0.0051	0.0093	0.0068		0.0431			0.0145	0.0818	0.87
Anchoa compressa	0.0142		0.0045	0.1127	0.2524	0.0485	0.0154		0.0075				0.4552	4.87
Gillichthys mirabilis		0.0001	0.0014		0.0889	0.0361	0.0102	0.0020					0.1387	1.48
Hypsopsetta guttulata					0.0082	0.0020							0.0102	0.11
Mugil cephalus	0.0006	0.0004										0.0003	0.0013	0.01
Anchoa delicatissima	0.0030	0.0002	0.0039	0.0084	0.0013		0.0001	0.0017					0.0186	0.20
Quietula ycauda						0.0011							0.0011	0.01
Engraulis mordax							0.0046	0.0003					0.0049	0.05
Cymatogaster aggregata				0.0074	0.0072	0.0023		0.0101	0.0009				0.0279	0.30
Ilypnus gilberti						0.1197							0.1197	1.28
Lepomis macrochirus	0.0008												0.0008	0.01
Monthly total	0.0194	0.0007	0.0105	0.1832	0.5647	1.0277	5.2120	0.0967	1.4490	0.6428	0	0.1455	9.3522 g DW m^{-2} yr	
													April-September 7.0948	75.86%

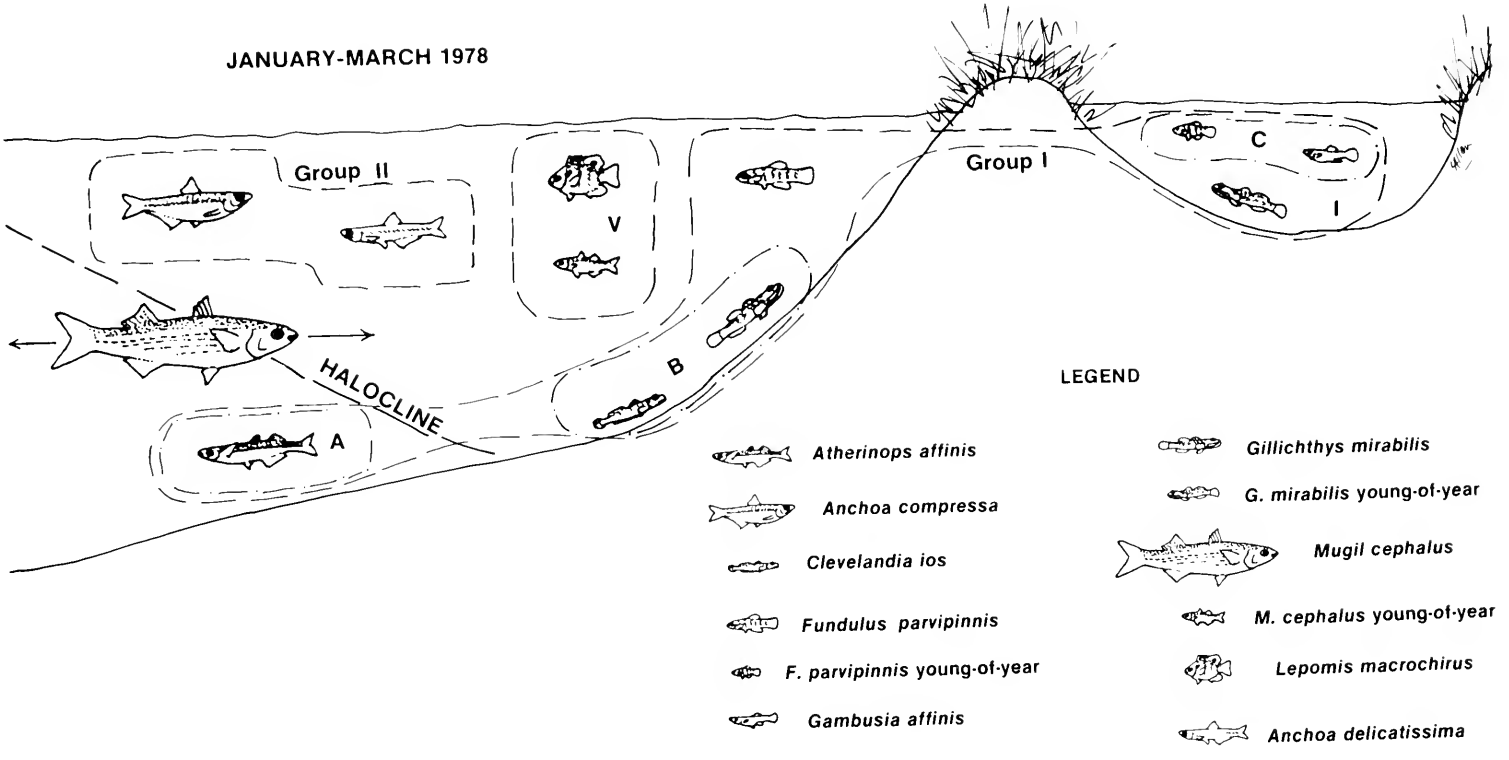

FIGURE 7.— Diagrammatic representation of the principal species inhabiting the littoral zone (alongshore and panne) of upper Newport Bay during January-March 1978. Inclusion level for species was ≥5 individuals in the samples during the period. Dashed lines enclose species from groups derived in the dendrogram of Figure 6. Arrows indicate inshore-offshore occurrence.

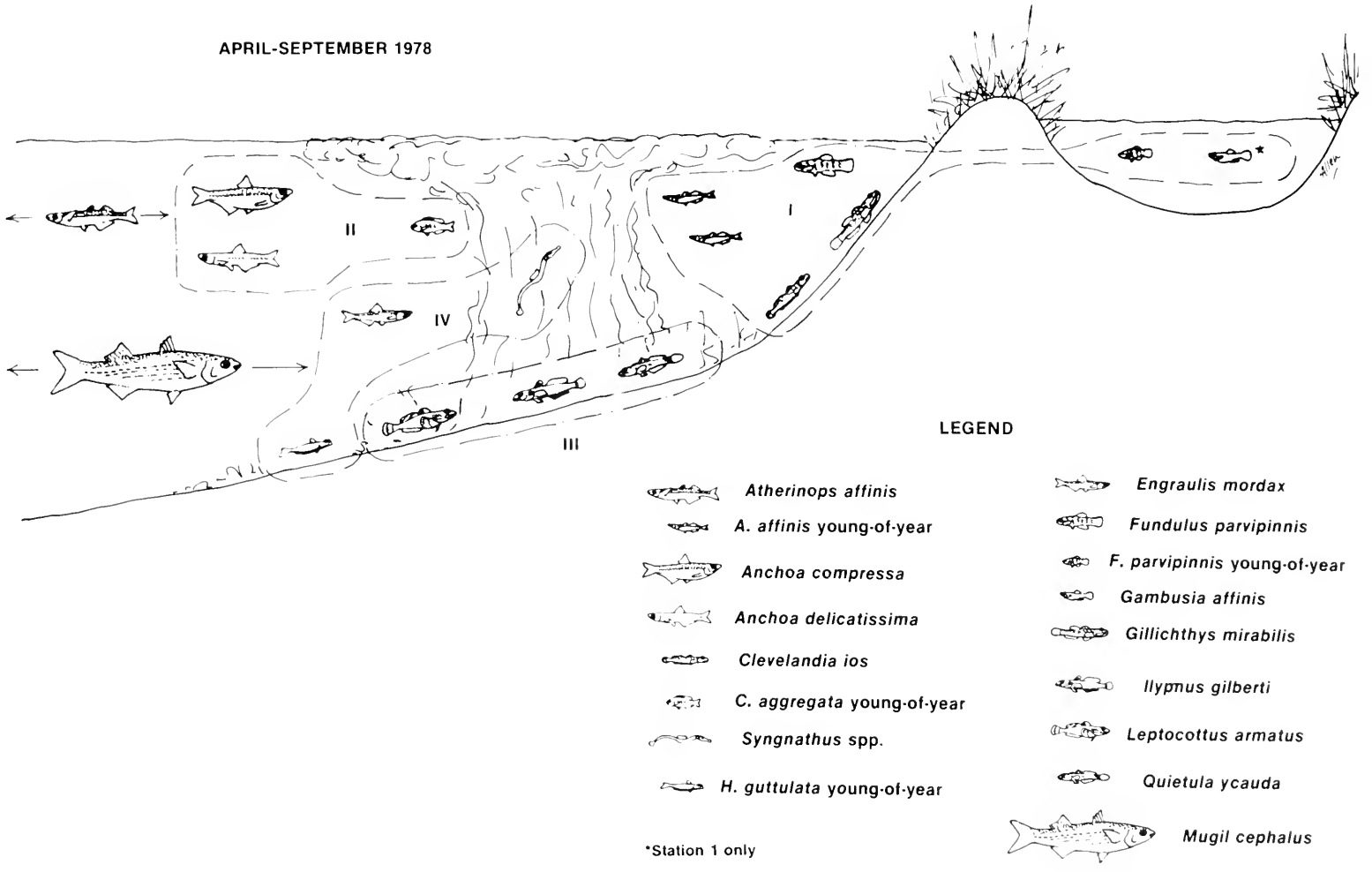

FIGURE 8.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during April-September 1978. Wavy vertical lines represent the large algal beds present during this period. Other information is the same as in Figure 7. (*Syngnathus* spp. includes *S. leptorhynchus* and *S. auliscus*.)

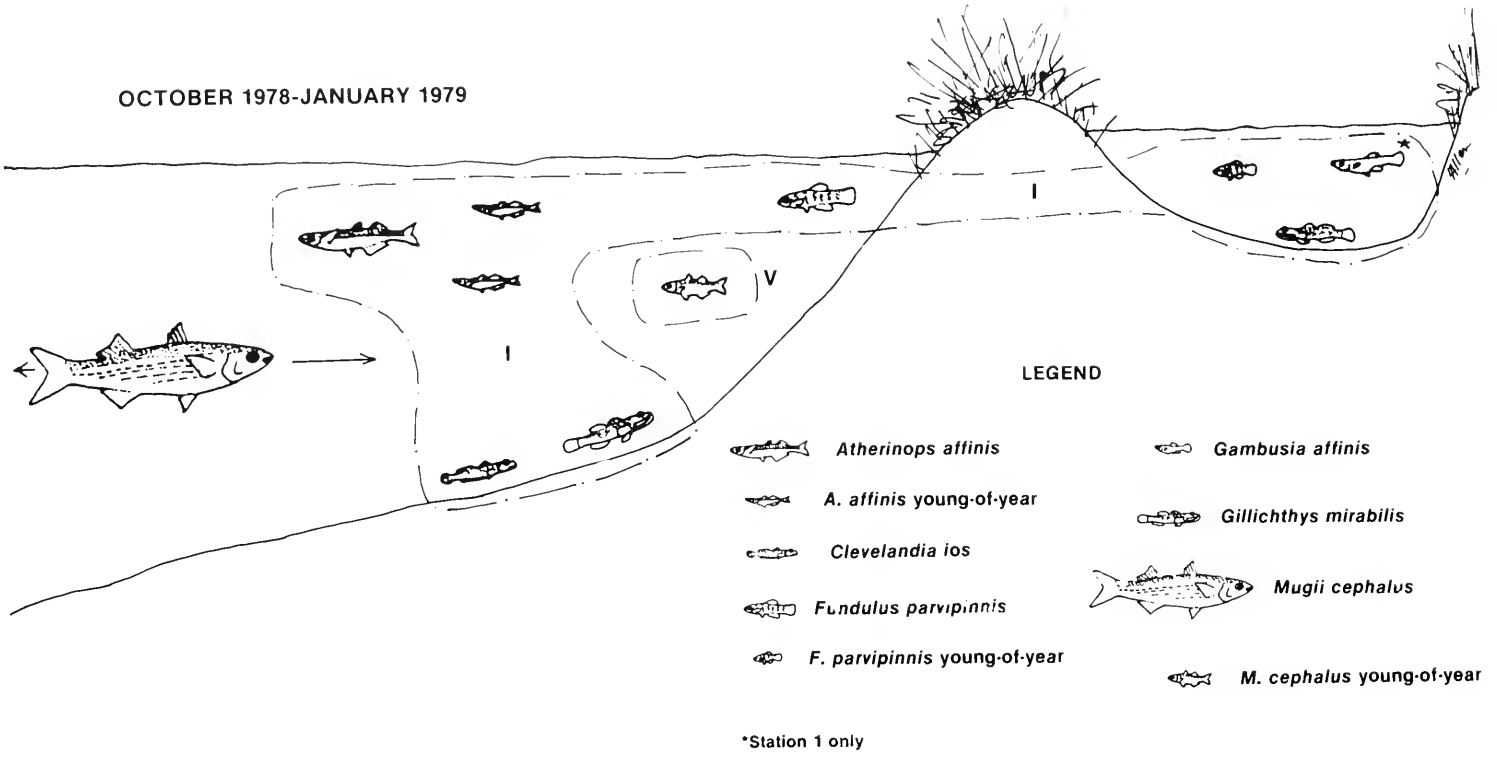

FIGURE 9.—Diagrammatic representation of the principal species inhabiting the littoral zone of upper Newport Bay during October 1978-January 1979. Other information as in Figure 7.

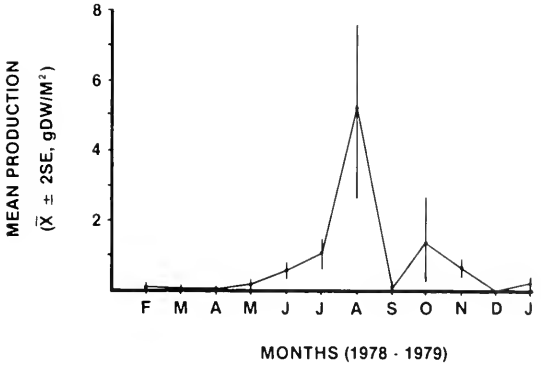

FIGURE 10.—Monthly variation in mean production ($\bar{x} \pm 2$ SE, g DW m^2) of the littoral fishes from three stations in upper Newport Bay (February 1978-January 1979).

low from February to May 1978, increased rapidly from June to a peak in August (5.2 g DW/m^2). Monthly production then declined drastically in September, a period of heavy rainfall during which many of the larger young-of-the-year *Atherinops affinis* emigrated from the study area. Production increased in October but then showed a steady decline to zero in December, a time of a sharp decrease in mean water temperature in the upper bay.

Relationship of Abiotic Factors to Fish Abundance and Distribution

Temperature was found to have a significant, positive correlation ($P<0.01$, df = 37) with number of species ($r = 0.42$), number of individuals ($r = 0.48$), and biomass ($r = 0.54$) when station totals were considered. Similarly, salinity was significantly correlated with number of individuals ($r = 0.36$) and biomass ($r = 0.64$) (Table 4).

Temperature was the factor which yielded the highest number of significant correlations (6) with individual species, followed by salinity, dissolved oxygen, distance into the upper bay, and depth of capture, each with four (Table 4).

An analysis of intercorrelations among abiotic factors yielded three significant ($P<0.05$, df = 37) positive relationships: 1) Temperature and salinity ($r = 0.48$); 2) temperature and dissolved oxygen ($r = 0.53$); and 3) dissolved oxygen and distance into the upper bay ($r = 0.32$).

According to canonical correlation analysis, the six abiotic variables accounted for 93% of the variation in individual species abundances along the first canonical axis (Table 5). A second run indicated that 83% of the variation in species abundances could be accounted for by temperature and salinity alone. This finding strongly implies that interactive effects of temperature

TABLE 4.—Correlation coefficients (r) of individual species numbers and of total number of species, number of individuals, and biomass with six environmental factors. TEMP = temperature, SAL = salinity, DO = dissolved oxygen, DSTUPB = distance into upper Newport Bay from Highway 1 bridge, APRTSZ = average particle size of sediments, DPTHCAP = depth of capture.

Species	Abiotic factors					
	TEMP	SAL	DO	DSTUPB	APRTSZ	DPTHCAP
Atherinops affinis	0.55**	0.57**	0.21	0.00	−0.12	0.23
Fundulus parvipinnis	0.18	0.15	−0.31*	0.00	−0.06	0.03
Anchoa compressa	0.38*	0.21	0.35*	−0.01	0.05	0.24
Clevelandia ios	0.43**	0.22	0.08	−0.09	−0.16	0.23
Mugil cephalus	−0.62**	−0.29	−0.10	0.11	0.26	0.02
Gillichthys mirabilis	0.25	−0.22	0.44**	0.31*	0.01	0.00
Anchoa delicatissima	0.10	0.08	−0.22	−0.22	0.05	−0.02
Gambusia affinis	0.21	−0.25	0.16	0.58**	−0.07	−0.02
Hypsopsetta guttulata	0.30	0.21	0.43**	0.26	−0.10	0.28
Cymatogaster aggregata	0.14	0.28	−0.01	−0.34*	0.01	0.14
Quietula ycauda	0.46**	0.35*	0.19	−0.16	0.01	0.35*
Ilypnus gilberti	0.39*	0.31*	0.23	−0.10	0.11	0.33*
Lepomis macrochirus	−0.29	−0.44*	−0.23	0.10	0.09	0.04
Lepomis cyanellus	0.06	−0.27	−0.29	0.16	−0.20	0.05
Engraulis mordax	0.22	0.16	0.00	0.13	−0.07	0.33*
Leuresthes tenuis	0.16	0.14	−0.09	−0.15	0.10	−0.01
Leptocottus armatus	0.29	0.13	0.38	−0.09	−0.01	0.05
Syngnathus spp.	0.53	0.23	0.35	0.08	−0.07	0.33*
Species totals (by station)						
No. of species	0.42**	0.05	—	—	—	—
No. of individuals	0.48**	0.36*	—	—	—	—
Biomass	0.54**	0.64**	—	—	—	—

* = significant at 0.05 level
** = significant at 0.01 level.

TABLE 5.—Summary of two canonical correlation runs of individual species abundances against environmental variables.

Axis	R^2	R	X^2	df
Run No. 1 (6 environmental; 18 species)				
1	0.93	0.96	212.9*	126
2	0.84	0.92	144.1*	102
3	0.73	0.85	96.3	80
Run No. 2 (temperature, salinity only, 18 species)				
1	0.83	0.91	77.8*	36
2	0.61	0.78	26.5	17

* = significant at 0.01.

and salinity were important in influencing species abundance.

The 18 most common species were ordinated along temperature and salinity axes using simple correlation values (r) as an index of relative influence of these two factors (Fig. 11). Thirteen of the 18 species were positioned in the upper right quadrant indicating that they were all positively correlated with temperature and salinity. Three species, *Gambusia affinis*, *Gillichthys mirabilis*, and *Lepomis cyanellus*, located in the upper left quadrant correlated positively with temperature, but negatively with salinity. The lower left quadrant includes two species, *Lepomis macrochirus* and *Mugil cephalus*, with negative temperature and salinity influences. No species were positioned in the negative temperature, positive salinity quadrant probably because this situation rarely occurred in the littoral zone in 1978.

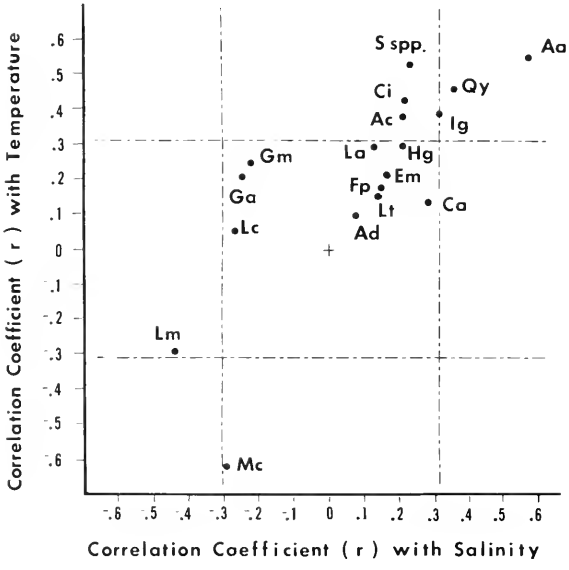

FIGURE 11.—Ordination of 18 common species of the littoral zone of upper Newport Bay on correlation coefficients (r) for temperature (y-axis) and salinity (x-axis). Dashed lines indicate 0.05 significance levels. Aa-*Atherinops affinis*, Ac-*Anchoa compressa*, Ad-*Anchoa delicatissima*, Ca-*Cymatogaster aggregata*, Ci-*Clevelandia ios*, Em-*Engraulis mordax*, Fp-*Fundulus parvipinnis*, Ga-*Gambusia affinis*, Gm-*Gillichthys mirabilis*, Hg-*Hypsopsetta guttulata*, Ig-*Hypnus gilberti*, La-*Leptocottus armatus*, Lm-*Lepomis macrochirus*, Lt-*Leuresthes tenuis*, Mc-*Mugil cephalus*, Qy-*Quietula y-cauda*, Sspp-*Syngnathus* spp.

DISCUSSION

Composition, Diversity, and Seasonal Dynamics

The ichthyofauna of the littoral zone in upper Newport Bay was numerically dominated by a few, low trophic-level species (five species accounted for >98% of all specimens collected), a situation similar to that found in many estuarine fish populations (Allen and Horn 1975). *Atherinops affinis* is an opportunistic feeder and has been characterized as both a herbivore/detritivore (Allen 1980) in upper Newport Bay and a low-level carnivore (Fronk 1969; Quast 1968). The second most abundant fish, *Fundulus parvipinnis*, is a low-level carnivore that feeds on small crustaceans and insects (Allen 1980; Fritz 1975). *Gambusia affinis*, *Clevelandia ios*, and *Anchoa compressa* are, likewise, low-level carnivores, feeding mainly on insects, benthic microinvertebrates, and zooplankton (Allen 1980).

Large individuals of *Mugil cephalus* were not sampled effectively, but probably constituted a significant proportion of biomass within these fish assemblages. Adult *M. cephalus* fed mainly on detritus and pennate diatoms (Allen 1980). This essentially herbivorous diet closely matches that described by Odum (1970) for *M. cephalus*.

The overall H' diversity values (H'_N range, 0.42-1.76; overall 0.89) for the littoral zone were comparable to values derived from other studies of bay-estuarine fish faunas and to other studies in Newport Bay. Haedrich and Haedrich (1974) derived values of 0.33-1.03 for Mystic River Estuary, Mass.; Stephens et al. (1974) presented indices of 0.65-2.08 for Los Angeles Harbor, Calif.; Allen and Horn (1975) published values of 0.03-1.11 for Colorado Lagoon, Alamitos Bay, Calif.; and Quinn (1980) calculated values of 0.21-2.59 (overall 1.9) for Serpentine Creek in subtropical Queensland. Using otter trawl data, I calculated H'_N values of 0.20-1.96 (overall 0.98) for the upper Newport Bay in 1974-75 (Allen 1976). The concurrent bimonthly portion of this study (Horn

and Allen 1981) obtained a bimonthly range for numbers of 0.48-2.17 (overall 1.05) when the deeper channel areas were also sampled. The relatively wide range of H'_N values in all of the above studies reflects the differential utilization of these embayments by fishes on a seasonal basis. At the same time, the low overall diversity reflects dominance both in numbers and biomass by a few species. The seasonal usage has the effect of increasing annual diversity, although only one or two species dominate numerically at any one time. The H' values for biomass (H'_B range 0.23-1.55; overall 0.84) were fairly close to those for numbers and, again, mainly reflected the dominance of *A. affinis* (~80%). In all, 26 of the 32 reported species had young-of-the-year fishes, making up a significant portion of their populations. Fluctuations in juvenile population levels had a substantial effect on the littoral fish populations. Juvenile recruitment plus the immigration of adult fishes presumably for reproduction or for exploitation of high productivity in warmer months were the principal causes for seasonal changes in the ichthyofauna. These activities reflect the widely recognized function of bay-estuarine environments as spawning and nursery grounds (Haedrich and Hall 1976).

The general pattern of increased number of species and numbers of individuals during the late spring through fall period in upper Newport Bay has been observed in many other studies of temperate bay-estuarine fishes (e.g., Pearcy and Richards 1962; Dahlberg and Odum 1970; Allen and Horn 1975; Adams 1976a). Several studies of estuarine fish populations have, in addition, detected summer depressions in abundance between peaks in spring and fall in other estuaries (Livingston 1976; Horn 1980) and in lower Newport Bay (Allen 1976).

Studies of subtropical estuarine fish populations have shown a trend in seasonal abundances that is 6 mo out of phase with the above observations. Fish abundances were highest during the winter months (November-March) in the Huizache-Caimanero Lagoon of Mexico due to increases in members of both demersal and pelagic fishes (Amezcua-Linares 1977; Warburton 1978). This coastal lagoon system is subject to a narrower range of temperatures over the year (18.3°-27.9°C) than most temperate systems. However, the Mexican system undergoes wide variation in salinity, especially during the rainy season from July to October (see section Influence of Abiotic Factors).

Species Associations

Species groupings were subject to strong seasonal influence and bore a striking resemblance to the classification scheme of Atlantic nearshore fish communities proposed by Tyler (1971). According to Tyler's classification the Atlantic nearshore fish communities can be divided into regular and periodic components. Periodic components can be winter seasonals, summer seasonals, or occasionals. The upper Newport Bay fish assemblage had regulars (group I) and periodics (groups II-V). The "anchovy" group (II), the "goby" group (III), and the "*Engraulis-Hypsopsetta*" group (IV) were all summer seasonals. Group V had both winter seasonals in *Mugil cephalus* and *Lepomis macrochirus* and summer seasonals in *Lepomis cyanellus* and *Leuresthes tenuis*. The latter group, however, could best be characterized by the affinity of its components to lower salinities rather than to a particular time of year. The occasional component was represented by the 12 species of group VI which also occurred in the summer. Thus Tyler's classification may have a broader application than he originally proposed, and perhaps holds true for many estuarine ichthyofaunas.

Species Densities and Productivity

Density estimates for some species of littoral fishes are particularly difficult to obtain. Such species include small, burrow-inhabiting fishes of the family Gobiidae and other small benthic fishes such as killifishes, flatfishes, and sculpins which escape under a seine or through the mesh of various nets. This study attempted to obtain density values for all littoral fishes, especially for the elusive species listed above. By setting up the procedure for choosing the "best estimate" of density from among four different sampling methods, actual densities of the species have been more closely approximated.

If the biomass density of *Atherinops affinis* for the entire study is calculated by dividing its total biomass by the total area of coverage by all four sampling gears, a biomass density of 3.3 g/m^2 (or about 0.83 g DW/m^2) is obtained. This density value is lower than the estimate of 1.16 g DW/m^2 derived through the best estimate process (Table 6). In this particular case, most densities were mean values of six bag seines which were very effective (99%) at capturing *A. affinis* (Horn and Allen footnote 2). Biomass density for the gobiid,

TABLE 6.—Grand mean estimate of biomass density (g DW/m^2) for common species in the littoral zone (excluding panne) over the 13-mo period (January 1978-January 1979) from the best estimate criteria.

Species	$\bar{X}$ g DW/m^2±1 SE
Atherinops affinis (adult)	0.1043±0.0602
A. affinis	1.1590±0.2573
Fundulus parvipinnis	0.1064±0.0223
Gambusia affinis	0.0015±0.0028
Clevelandia ios	0.0261±0.0117
Anchoa compressa	0.1195±0.0493
Cymatogaster aggregata	0.0167±0.0158
Gillichthys mirabilis	0.0131±0.0035
Anchoa delicatissima	0.0077±0.0053
Mugil cephalus	0.0024±0.0018
Quietula ycauda	0.0029±0.0025
Ilypnus gilberti	0.0021±0.0021
Hypsopsetta guttulata	0.0043±0.0035
Engraulis mordax	0.0019±0.0018
Lepomis macrochirus	0.0006±0.0005
Lepomis cyanellus	0.0003±0.0001
	1.5688 g DW/m^2

Clevelandia ios, determined by total area coverage was 0.013 g/m^2 (about 0.003 g DW/m^2). The value based on best estimate (using square enclosures and small seine estimates) was about 10 times higher at 0.03 g DW/m^2. This large discrepancy is due to the low efficiency of the bag seine for capturing this species. Since the bag seine covered the largest area of any of the sampling gears (220 m^2), its addition to the density determination for *C. ios* led to the large underestimate. The total biomass density of all species by total area was 4.13 g/m^2 (or about 1.02 g DW/m^2) which again was lower than the best estimate grand mean density of 1.57 g DW/m^2.

Average standing stock for the upper bay species during 1978 was 784 kg DW, based on an estimate of 50 ha of habitable littoral zone in upper Newport Bay. This is equivalent to 3,136 kg (wet weight) or 6,899 lb of fish. By the same procedure, the average standing stock of *A. affinis* was 631.6 kg DW and that of *C. ios*, 13.1 kg DW.

The annual production of 9.35 g DW/m^2 for the upper Newport Bay littoral zone in 1978 ranked among the highest values recorded for studies with comparable production determinations of production models (Table 7).

The Newport Bay production estimate in 1978 was surpassed only by the estimate for *Fundulus heteroclitus* (Meredith and Lotrich 1979), an estuarine species of the east coast of the United States. *Fundulus heteroclitus* represented a very efficient energy link between the marsh and the littoral zone in their study. However, as Meredith and Lotrich pointed out, the production value may be an overestimation due to the underestimation of the area of marsh utilized by the fish. The value 4.6 g DW/m^2 obtained by Adams (1976b) for fishes inhabiting east coast eelgrass beds, which are acknowledged as highly productive areas, is half the estimate for the littoral zone of upper Newport Bay.

Short food chains have been implicated as the primary reason for high production in estuarine fish communities (Adams 1976b), a contention which is supported by the findings of this study. Young-of-the-year *Atherinops affinis* accounted for 85% of the annual production and formed a direct link through their herbivorous/detritivorous diet to the high primary productivity of this estuarine system. The remaining, numerically important species of the littoral zone were low-level carnivores. There is little doubt that this assemblage represents an example of "food chain telescoping" as described by Odum (1970).

Even though the fish production in the littoral zone of upper Newport Bay was high compared with most comparable studies, the value presented here is undoubtedly an underestimate. The largest species of the system, adult *Mugil cephalus*, was not represented in the production estimates due to inadequate sampling. Inclusion of this species would have substantially increased the production value. It is unlikely, however, that productivity of adult *M. cephalus* could approach that of juvenile *Atherinops affinis* which were responsible for 85% of the annual fish production.

Influence of Abiotic Factors

The positive correlations between temperature and total abundance, biomass and number of species, and between salinity and total abundance and biomass indicate the general impor-

TABLE 7.—Comparison of annual fish production (P) for marine or estuarine studies with comparable production determinations. Wet weights were converted by multiplying by 0.25. Values are for all species except where noted.

Locale and habitat	Study	Estimated annual P (g DW/m^2)
Delaware salt marsh creek (*Fundulus heteroclitus*)	Meredith and Lotrich (1979)	10.2
Newport Bay littoral zone	present study	9.4
Mexican coastal lagoon	Warburton (1979)	8.6
Cuban freshwater lagoons	Holčik (1970)	6.2
No. Carolina eelgrass beds	Adams (1976b)	4.6
Bermuda Coral Reef	Bardach (1959)	4.3
Texas lagoon (Laguna Madre)	Hellier (1962)	3.8
English Channel pelagic and demersal fishes	Harvey (1951)	1.0
Georges Bank commercial fishes	Clarke (1946)	0.4

tance of these factors to this assemblage. Individual correlations between abiotic factors and species abundances likewise emphasized the importance of temperature and salinity. The correlations between individual species abundances and dissolved oxygen as well as distance into the upper Newport Bay could be due to the intercorrelations of both dissolved oxygen and distance with temperature.

Intercorrelations among factors can confound the interpretation of relationships and introduce redundancy in multivariate analyses. The relationship between dissolved oxygen and distance into the upper Newport Bay is intuitive considering its shallow depths. The positive relationship between temperature and dissolved oxygen was probably due to photosynthesis by green algae during the summer. Winter rainfall in the basically Mediterranean climate of southern California was responsible for the positive correlation between temperature and salinity found in Newport Bay. This relationship is by no means absolute, as evidenced by the low salinities encountered during the tropical rains of September 1978 when temperatures were high.

The results of the second canonical correlation analysis indicate that interaction between temperature and salinity explained most of the variability in species abundance in this system. The correlation between these two abiotic factors probably inflated the R^2 value slightly, but does not negate the overall findings. Ordination of individual species by correlation coefficients with temperature and salinity underscores the influences of these factors on individual species. Furthermore, the substantial decrease in numbers of *A. affinis* at station 1 and the somewhat smaller decrease at station 3 during September rains (low salinity) and relatively high temperatures also illustrate this temperature-salinity interaction.

I propose that an important consequence of temperature-salinity influence found in the present study is the transfer of biomass and, therefore, energy from the littoral zone to the adjacent channel and ultimately to local offshore areas via migration of fishes. This mechanism for energy transfer was best illustrated by the apparent emigration of a large portion of the 0-age class *A. affinis* from the littoral zone from September to December 1978. The transfer also included the biomass produced by essentially all of the periodic species. Weinstein et al. (1980) reached a similar conclusion in their study of the fishes in shallow marsh habitat of a North Carolina estuary. An extensive mark and recapture study should be planned to test this hypothesis in the future.

Seasonal fluctuations of temperate bay-estuarine fish populations may have several causes, but temperature and salinity seem frequently to be the underlying factors. The pattern of increased number of species and individuals with increased temperature in temperate bays and estuaries has been reviewed by Allen and Horn (1975). Recently the large-scale influence of salinity on bay-estuarine fish populations has been demonstrated by Weinstein et al. (1980) for Cape Fear River Estuary, N.C. Unfortunately, any salinity interaction with temperature was not investigated or discussed in the above study.

Studies of subtropical estuaries (Amezcua-Linares 1977; Warburton 1978; Quinn 1980) indicate that salinity may have greater influence on fish populations, since annual temperature ranges are narrower than in temperate bays and estuaries. In each of the above studies on subtropical estuaries, increased abundances corresponded to the season of low rainfall and therefore high salinity. Blaber and Blaber (1981) concluded that turbidity and not temperature and salinity was the single most important factor to the distribution of juvenile fishes in subtropical Moreton Bay, Queensland. However, Blaber and Blaber (1981) did not present statistical evidence to support this contention. The most important environmental factors influencing tropical estuarine (eelgrass) ichthyofaunas are more difficult to identify (Weinstein and Heck 1979; Robertson 1980) and probably include biotic factors such as prey availability, competitors, predators, as well as abiotic factors. Biotic interactions are undoubtedly important in temperate estuarine systems including upper Newport Bay. However, their overall influence on the system is probably swamped by large fluctuations in the physical environment.

Fluctuations in rainfall and temperature regimes during a year and from year to year can have marked effects on the ichthyofauna of estuaries. Moore (1978) has identified long-term (1966-73) fluctuations in summer fish populations in Aransas Bay, Tex. He found that diversity values (H' range of 1.38-2.13) were quite variable from year to year probably as a result of major climatological changes (an unusually wet year; a drought and two hurricanes). These changes in diversity values were probably caused

by changes in abundance within a set of resident estuarine species and of periodic species.

In 1978 the ichthyofauna of upper Newport Bay was subjected to rainfall twice that of a "normal" year (70.9 cm for 1978; mean 28.1 cm). The specific effects of this increased precipitation are difficult to assess due to a lack of data from previous years but some guarded comparisons can be made. Population densities of *Atherinops affinis* were lower in 1974-75 than those encountered during 1978 (Allen 1976). Also *Cymatogaster aggregata*, *Clevelandia ios*, and *Leptocottus armatus* occurred in lower numbers in 1978 than in previous years (Horn and Allen 1981). These discrepancies point out the strong year-to-year fluctuations that occur in the fish populations of upper Newport Bay. This conclusion is in complete agreement with the findings of Moore (1978) and sheds doubt on the possibility of completely characterizing a "normal" year in many estuaries because of unpredictable annual variations in climate.

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CYCLIC COVARIATION IN THE CALIFORNIA KING SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, SILVER SALMON, *O. KISUTCH*, AND DUNGENESS CRAB, *CANCER MAGISTER*, FISHERIES

LOUIS W. BOTSFORD,[1] RICHARD D. METHOT, JR.,[2] AND JAMES E. WILEN[3]

ABSTRACT

There are apparent cyclic fluctuations in the catch record of both northern and central California salmon fisheries. They are of the same period and strength as well-known cycles in crab catch but of different phase. Statistical characteristics of this covariation, as reflected in estimates of auto- and cross-correlation functions, change following the decline of the central California Dungeness crab fishery. Analysis of a likely cause of this phenomenon, a greater delay in switching of effort from crab to salmon during years of high crab catch, indicates that this mechanism is not present. Phase differences between salmon and crab cycles imply constraints on remaining potential causes, but a cause of the cyclic covariation has not been established.

Regular patterns in fishery catch records reflect underlying mechanisms that can provide the basis for broader understanding, better prediction, and consequently better management of the fishery. Cyclic fluctuations in the northern California Dungeness crab catch have been a topic of research for the past 10 yr. We document here cyclic fluctuations in the northern California salmon catch (Fig. 1) of the same frequency but different phase.

Coastwide fluctuations in Dungeness crab catch were originally attributed to oceanographic causes (Anonymous 1965). Peterson (1973) demonstrated a statistical relationship between coastal upwelling and crab catch. Botsford and Wickham (1975) concluded from estimates of the appropriate cross- and auto-correlation functions that, while crab catch was indeed cyclic and upwelling was correlated with crab catch after a lag of 1 or 2 yr, upwelling itself was not cyclic, hence was not the source of the cycles. Botsford and Wickham (1978) later showed that interage, density-dependent mortality could be the cause of the observed cycles, and derived new stability results that indicated size-selective fishing could decrease population stability, and thereby increase the propensity for cyclic fluctuations. They cited two known potential interage, density-dependent mechanisms, cannibalism and an egg-predator worm, and are conducting field samples of these. On the basis of a disparity between the period of observed cycles and the period of cycles produced by a model that included cannibalism, McKelvey et al. (1980) claimed that cannibalism could not cause the cycles. Botsford (1981) pointed out that the observed disparity was not new, but had been noted by Botsford and Wickham (1978), and critically analyzed the reasoning used by McKelvey et al. (1980) in drawing a new conclusion. In summary, the cause of cycles in the northern California Dungeness crab

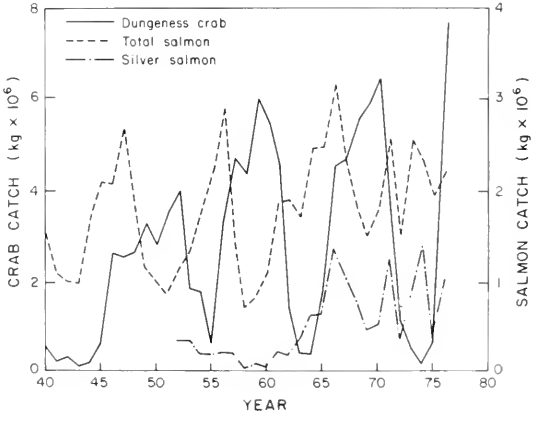

FIGURE 1.—Total landings (kg) in the northern California crab and salmon fisheries for the years 1940-76.

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catch record is still not known and research in this area is continuing.

In contrast to the considerable research attention attracted by cyclic fluctuations in crab catch, fluctuations in the salmon catch record have, to our knowledge, not been previously identified as cyclic. Yet, as seen in Figure 1, these apparently periodic fluctuations in salmon catch have a peak amplitude of about ±0.5 of the mean value. While abundance is predicted each year as part of the management process, these predictions have not taken advantage of this regular pattern that accounts for about two-thirds of the peak catch. An understanding of the underlying cause of cycles in salmon catch has great potential for improved predictive ability and better salmon management.

There are many possible causes of the observed similar cycles in the salmon and crab fisheries. There may be a direct biological interaction between the two species that by itself gives rise to cycles. Alternatively, one may vary cyclically and a direct biological interaction may cause the other to follow it. As another class of possibilities the two processes need not necessarily be directly related but may both be under the influence of a third process (e.g., environmental factors). A third class of possible causes of the observed covariation is some sort of economic linkage between the two fisheries. Since many fishermen fish both species, abundance and effort in one could affect effort in the other.

METHODS AND DATA

Our approach to eliminating unlikely causes of the observed covariation from the many possible causes is based on interpretation of estimated auto- and cross-correlation functions (also called correlograms). This statistical technique has been useful in interpretation of cycles in wildlife populations (Moran 1949; Finerty 1980) and is a recommended initial step in time series analysis (Jenkins and Watts 1968; Box and Jenkins 1970). However, there are few useful results on statistical significance of estimated correlation functions. We use a simple form of a method described by Bartlett (1946). If individual points in a time series are independent and identically distributed, an estimate of the correlation between them is Gaussian with mean zero and variance $1/N$ where N is the total number of samples on which the estimate is based. In the following analysis we show 5% error limits on plots of correlation functions. The occurrence of values of correlation greater in magnitude than this limit more frequently than 1 in 20 indicates a "nonrandom" process. This approach is somewhat limited in that it focuses on single points rather than the pattern of the estimated correlation function as a whole.

If samples in each series are not independent, the significance of both cross- and auto-correlation functions will be overestimated (Granger and Newbold 1974). A suggested solution to this problem in estimating cross-correlations is to prewhiten (i.e., remove correlation between samples) each series by fitting an ARMA model (Box and Jenkins 1970) to the series, then compute cross-correlations between the residuals. We have not taken this approach for two reasons: 1) Computed correlations based on the residuals actually underestimate significance of results (Box and Pierce 1970; Durbin 1970) and 2) prewhitening may actually remove correlations of real interest. With regard to the latter, some auto-correlation within each series exists because of known physical processes (e.g., the fact that catch is the result of fishing several age classes causes intraseries correlation). Removal of this intraseries correlation would reduce the chance of detecting real interseries correlation (e.g., correlation stemming from a causal mechanism that involved catch). Removal of intraseries correlation on the basis of known physical mechanisms will provide more meaningful results; however, it will require further studies of effort dynamics and life histories in both the salmon and crab fisheries. In the meantime, as a simple exploration of the possibility of "spurious" results, we also present correlograms computed from first-differenced data (first-differencing is the process of replacing the data point x_t at time t with the difference $x_t - x_{t-1}$). First-differencing reduces intraseries correlation and has been shown to greatly reduce the incidence of spurious interseries correlation (Granger and Newbold 1974). Correlation results of first-differenced data can be interpreted as the correlation between changes in each series. Also, in all correlations presented, a linear trend has been removed from the series.

Salmon data for these analyses are from monthly catch records collected and published by the California Department of Fish and Game (1954-78). The northern California salmon catch consists of landings at Crescent City, Eureka, and Fort Bragg. The central California catch is from

San Francisco and Monterey. The unit of salmon catch is kilograms of dressed fish with heads on.

Crab catch (kilograms) was summarized by season rather than calendar year so that a season's catch includes catch from November and December of the previous year. The geographic breakdown of crab catch was the same as the salmon catch. Seasonal distribution of crab catch and effort was available only from 1952 to 1976[4] for a northern California region which included an average of 93% of the total northern California catch. In addition to crab catch data, we have also used recent estimates of preseason legal abundance (Methot and Botsford 1982). These estimates were computed from the decline in catch-per-unit-effort within each season according to the Leslie method. Gotshall (1978) also estimated preseason legal abundance for the years 1967-72 using the Leslie method. His results for those years are essentially the same as those used here. McKelvey et al. (1980) also estimated preseason legal abundance, but used a method that depended on the estimated total number of pots in the fishery and annual catch. Since the relationship between these variables can change from year to year in this fishery, we did not use their estimates.

We present first the statistical characteristics of cyclic fluctuations in the northern California salmon and crab catch records as reflected in estimates of their auto- and cross-correlation functions. We then examine characteristics of each of the two salmon species in the fishery. The northern California salmon fishery is composed of king (or chinook) salmon, *Oncorhynchus tshawytscha*, which originate primarily in coastal rivers of northern California and Oregon, and silver (or coho) salmon, *O. kisutch*, which originated primarily in coastal rivers of northern California and Oregon in the 1950's, but depend increasingly on hatchery production in Oregon in the 1960's and 1970's (Pacific Fisheries Management Council 1978).

We then compare the characteristics of the northern California fishery to the central California fishery which differs in two respects: 1) It includes a period of protracted decline in the crab fishery and 2) it involves salmon stocks that originated in the Sacramento and San Joaquin River systems (Pacific Fisheries Management Council 1978). The central California crab fishery declined near 1960 and has remained at a low level since then. Putative causes of this decline and continued low level include an increase in sea temperature (Wild 1980), a predatory worm (Wickham 1979), and an increase in individual growth rate (Botsford 1981). We compare characteristics of the northern California fisheries with the central California fishery both before and after the decline.

We then examine a specific potential cause of the observed covariation. The most obvious and perhaps the most parsimonious explanation of the observed covariation in catch records is switching behavior of fishermen. The proposed hypothesis is simply that, during years of high crab abundance, more fishermen continue to fish for crab rather than beginning to fish for salmon when the salmon season opens. The legal crab season opened in December and continued at least through June in the years of interest. The salmon season opened in April or May, depending on year and species. Although most of the crab catch is landed early in the season, crab and salmon seasons do overlap, thus providing an opportunity to switch. The possibility that this mechanism is responsible for the observed behavior is examined here from three points of view: 1) A comparison of catch during overlapping and nonoverlapping segments of the salmon season, 2) analysis of changes in mean date of the salmon catch, and 3) calculation of the relationship between salmon catch and crab catch per delivery during May and June.

RESULTS

Northern California Total Catch

Estimates of the auto-correlation function for both total northern California Dungeness crab landings and total northern California salmon landings for the years 1940 to 1976 are of the form that would arise from cyclic processes of period 9 or 10 yr (Fig. 2). They both fall to a significant negative value of correlation then rise to a significant positive value of correlation.[5] The auto-correlation of crab abundance is not shown

[4]Annual Market Crab-Statewide Reports, California Department of Fish and Game, 1952-77.

[5]Estimates of the same functions for the time period 1952 to 1976 imply that crab is more cyclic (dropping to 0.7 then increasing to 0.8) while salmon is less cyclic (dropping to −0.3 then increasing to 0.4). In this analysis, as in the raw data (Fig. 1), salmon catch appears to be more cyclic in earlier rather than later years, while the crab catch appears to be more cyclic in later years.

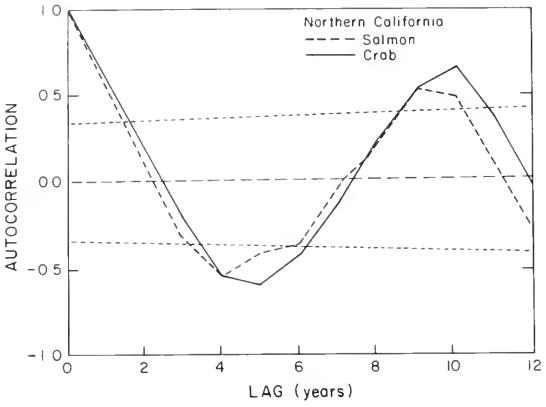

FIGURE 2.—An estimate of the autocorrelation functions for northern California total salmon and crab catch data (Fig. 1). Dotted lines are 0.05 error limits (see text).

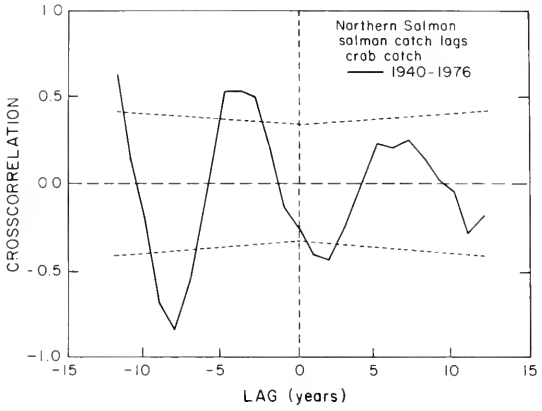

FIGURE 3.—An estimate of the cross-correlation function between northern California total salmon and crab catch data (Fig. 1). A positive lag corresponds to salmon following crab.

but is essentially the same as the auto-correlation of catch (i.e., decreases to significant negative values at 4 and 5 yr, then increases to significant positive values at 10 yr).

The auto-correlation functions computed from first-differenced crab and salmon catch series have the same form but are lower in absolute values. The first negative peak is just barely significant in both, whereas the positive peak of about 10 yr is significant only for the crab catch series.

An estimate of the cross-correlation between total northern California salmon and crab catch is of the form that would arise from two cyclic, covarying processes with a period of 9 or 10 yr and a constant lag of about 4 yr (salmon leading crab) (Fig. 3). Decreasing amplitude of the correlation function with increasing lag is caused by the increasing amplitude of crab catch. The implications of Figure 3 are that crab catch is negatively correlated with salmon catch 1 or 2 yr later and salmon catch is positively correlated with crab catch 3, 4, and 5 yr later.

The same cross-correlation computed for the years for which crab abundance estimates are available (1952-76) is essentially the same as Figure 3. The cross-correlation computed using preseason abundance instead of catch also is quite similar. First-differencing all three cross-correlation functions reduces the amplitude of the function somewhat. The correlation at positive lag is no longer significant and correlation at negative lag is significant only at a lag of −5 yr (except for first-differenced preseason abundance which is not quite significant). The values of cross-correlation for the various versions of these time series are summarized in Table 1.

Northern California Catch by Salmon Species

Because of differences in life history between the two species and the fact that increasing numbers of silver salmon originate in hatcheries, comparison of the relative contributions of each species to the cyclic covariation with crab could provide a clue to the underlying cause. Neither of the estimated auto-correlation functions for king and silver salmon appear as cyclic as the auto-correlation of combined salmon catch (Fig. 4). From this figure king salmon appears somewhat

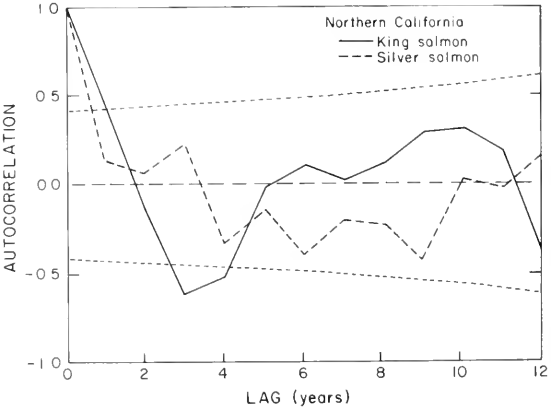

FIGURE 4.—An estimate of the autocorrelation functions for northern California king salmon and silver salmon catch data (Fig. 1) for the years 1952-76.

TABLE 1.—Cross-correlation between salmon catch and crab catch. Positive lags correspond to salmon following crab. Correlations are calculated from detrended original series (O) and from detrended, first-differenced series (F). Tabulated values are multiplied by 100 and are underlined if significant at the 5% level.

Region	Years	Variables		Lag																		
				-9	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8	9
North	40-76	Crab	Salmon	O	-68	-84	-55	-02	53	53	49	19	-14	-25	-41	-44	-25	00	22	20	24	15	02
				F	-40	59	-26	00	49	17	28	01	-20	03	-16	-25	-05	08	30	-08	17	-01	-10
North	52-76	Crab	Salmon	O	72	-90	-62	03	69	60	61	20	-18	-30	-46	-42	-13	19	43	33	29	09	-09
				F	50	-55	-33	08	57	14	39	-06	-24	06	-24	-28	-05	07	40	-03	19	-04	-17
North	52-76	Crab[1]	Salmon	O	59	83	64	-02	66	45	58	21	-16	-20	-40	-48	-15	16	35	35	20	09	-09
				F	-25	-45	-34	06	50	07	39	-08	-21	17	-16	-38	-01	09	24	09	01	08	-15
North	52-76	Crab	Salmon[2]	O	-48	-71	-49	-04	42	51	77	19	-35	-32	-52	-39	-01	17	48	40	40	-06	-36
				F	-29	-42	-13	03	19	17	51	-08	-38	14	-23	-23	18	-12	31	-06	35	-14	-31
North	52-76	Crab	Salmon[3]	O	68	-77	54	07	67	49	34	15	-03	-20	-29	-32	-18	16	28	19	15	16	11
				F	-48	-44	-37	09	67	05	13	-01	-02	-04	-16	-21	-22	21	32	01	-02	06	01
North	52-76	Crab	King	O	69	-80	-45	18	62	60	50	-04	-11	-36	-45	-26	03	31	43	22	08	-10	-15
				F	-45	-45	-19	17	49	31	27	-31	08	-12	-35	-14	-01	11	39	-04	05	-15	-05
North	52-76	Crab	Silver	O	-30	-47	-47	-21	34	22	38	42	-17	-02	-17	-38	-29	-10	15	27	41	30	05
				F	-21	-29	-27	-09	26	-17	26	28	44	22	06	-24	-06	-03	14	-00	22	12	20
Central	40-61	Crab	Salmon	O			-25	-19	16	64	81	33	-11	66	50	-05	09	26	34	27	00		
				F			-01	-09	18	15	12	16	06	59	18	33	18	24	-07	10	13		
Central	62-76	Crab	Salmon	O					92	-06	-47	-53	-29	24	-01	08	10	38	28				
				F					95	-40	-28	-25	-09	45	-10	08	-12	07	20				

[1]Abundance.
[2]Early season.
[3]Late season.

cyclic while silver salmon is less so. The latter may be due to the shorter time record for silver salmon. First-differencing decreases the value of the peak of negative correlation in king salmon to an insignificant level but the pattern is preserved.

Estimates of cross-correlation between crab catch and catch of each salmon species appear similar to the correlation between crab catch and total salmon catch (Fig. 5). Again, the observed characteristics seem to be stronger in the king salmon rather than the silver salmon records. First-differencing of the crab and salmon series reduces correlation values so that the positive correlation at a negative lag remains significant for king salmon only (Table 1).

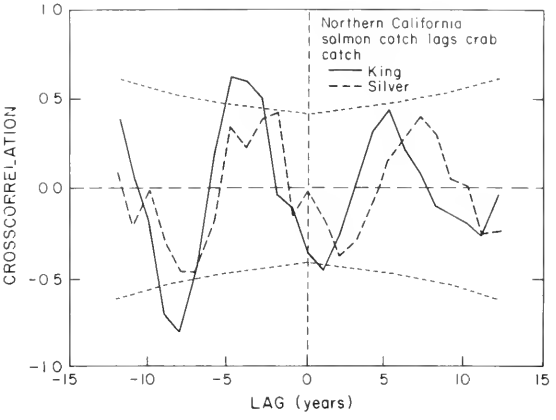

FIGURE 5.—An estimate of the cross-correlation function between northern California crab catch and king salmon and silver salmon for the years 1952-76.

Central California Total Catch

Because of differences between the central California crab fishery (Fig. 6) and the northern California crab fishery, comparison of characteristics of covariation between salmon and crab in northern California with that in central California provides some basis for determining the underlying cause of the covariation in northern California. We can narrow the range of possible causes by determining whether the covariation under discussion here exists both before and after the decline of the crab fishery in 1961. This investigation is, however, somewhat hampered by the extremely short time series that result from bisecting these records.

For the predecline period (1940-61), the auto-

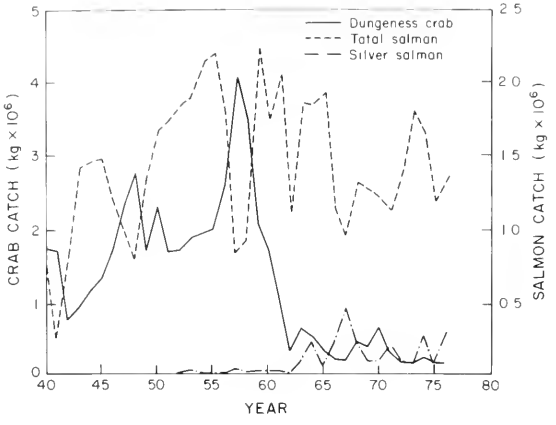

FIGURE 6.—Total landings (kg) in the central California crab and salmon fisheries for the years 1940-76.

correlation functions of salmon and crab catch are virtually the same as in northern California. Salmon and crab fall to −0.37 and −0.59, respectively, (the latter is significant at 0.05) at 4 yr, then increase to +0.43 and +0.54, respectively, (neither significant at 0.05) at 10 yr. First-differencing decreases the strength of both the positive and negative peaks of auto-correlation in both of these series. The estimated cross-correlation between salmon and crab catch in the early period is also similar to that in northern California except for a shift in the negative lag direction near zero lag (Fig. 7). The correlation at zero lag has a significant negative value in central California whereas it is not significant in northern California. This shift would correspond to a negative relationship between crab and salmon, with salmon following crab more closely in central than in northern California. After first-differencing each series the positive correlation peak at negative lag disappears but the negative correlation at zero lag remains (Table 1).

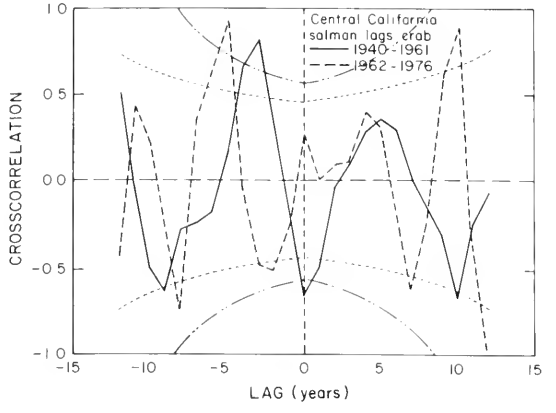

FIGURE 7.—Estimates of cross-correlation functions between central California Dungeness crab and total salmon catch, both before and after the decline in 1961. Outer significance levels apply to the period after the decline.

For the postdecline period (1962-76), the auto-correlation function for crab catch appears cyclic, as it was before the decline, but the period of the cycles has apparently decreased (Fig. 8). The auto-correlation function for salmon decreases to a significant negative value at 3 yr, but shows no clear cyclic tendency for greater lags. First-differencing decreases this first peak by about 0.1 for both series. The cross-correlation estimate for the postdecline period is similar to the northern California relationship for negative lags (i.e., crab following salmon), but is not similar for zero and positive lags (Fig. 7). Both of these latter estimates are for a low number of data points, hence interpretation for large lags is risky (note that the outer significance levels in Figure 7 are for the later period correlation). After first-differencing only the positive correlation at negative lag remains significant (Table 1).

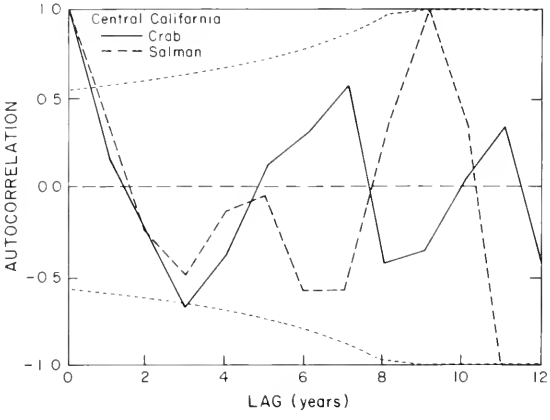

FIGURE 8.—An estimate of autocorrelation functions for central California Dungeness crab and total salmon catch for the years following the decline in crab catch (i.e., 1962-76).

Switching Effort Between Species

If the cyclic nature of salmon catch is caused by fishermen fishing salmon only when crab are not abundant, then cycles in salmon catch should be determined by salmon catch in the part of the

season that overlaps the crab season. In other words, salmon catch should appear to be much more cyclic early in the season than late in the season. Salmon catch for the months of April through June and the period from July through September are shown in Figure 9.[6] The only readily apparent feature of this plot is the increasing trend of early season catch.

Estimates of the auto-correlation functions of early and late season salmon catch are shown in Figure 10. Neither of these appears as smoothly cyclic as the total catch. However, since they both decrease to negative values then increase to approximately the same positive value at a 10-yr lag, one does not appear more cyclic than the other.

Estimates of the cross-correlation between total crab catch and early salmon catch and between total crab catch and late salmon catch are shown in Figure 11. There is very little difference between these functions for each time period and they are quite similar to the same function for total annual catch. The only difference between the two species is a slightly more pronounced pattern of correlation for early rather than late season to the right of the origin (i.e., where salmon follows crab). After first-differencing only the positive correlation at a lag of −5 remains (Table 1).

From Figures 10 and 11 we can conclude that the cyclic nature of salmon catch is not contained entirely in the early, overlapping part of the season.

A second, though not independent, means of testing the proposed hypothetical mechanism is to examine the mean data of salmon catch. If crab abundance determined salmon catch early in the salmon season, mean date of the salmon catch would increase with crab catch. The correlation between mean date of salmon catch and total crab catch was not significant ($r = -0.022$ with linear trend subtracted from mean date of salmon catch). Thus this test also yields a negative result.

A third consequence of the proposed mecha-

[6]The same analysis as that presented here was performed with a bisecting date of 31 May rather than 30 June with no difference in the results.

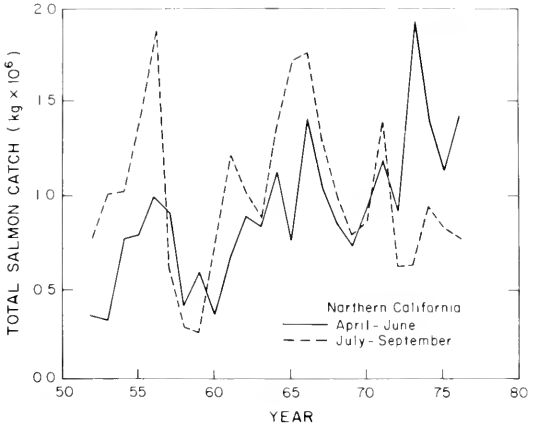

FIGURE 9.—Total salmon catch (kg) in northern California in the early part of the season (April-June) and the late part of the season (July-September) for the years 1952-76.

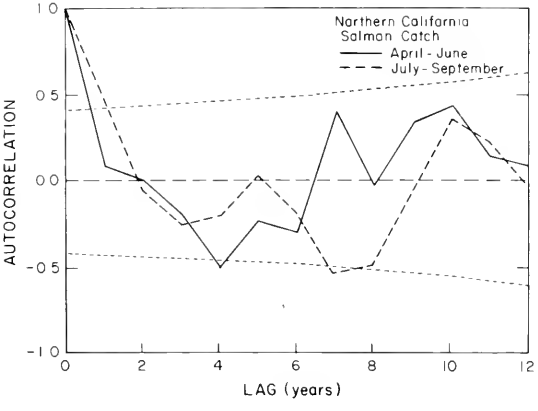

FIGURE 10.—Estimates of the autocorrelation functions for the early (April-June) and late (July-September) parts of the season.

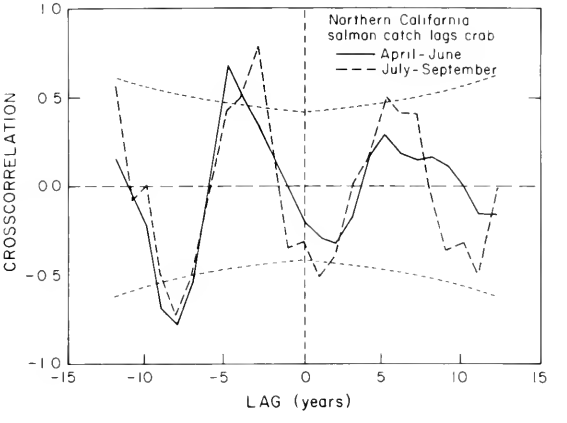

FIGURE 11.—Estimates of the cross-correlation functions between Dungeness crab catch and total salmon catch early in the season (April-June) or total salmon catch late in the season (July-September).

nism is a relationship between catch per delivery of crab and salmon catch. If fishermen continue to fish crab when crab is abundant, then there would be a relationship between catch per crab delivery and salmon effort in months of overlap between the two fisheries. This relationship would show up in salmon catch provided it was not occluded by fluctuations in salmon abundance. The value (v) per delivery of crab catch was computed for the months of May and June each year as follows:

$$v = \frac{P \cdot W}{CPI \cdot D}$$

where P = market price
W = total weight landed in the months of May and June
CPI = consumer price index
D = number of deliveries in the months of May and June.

For the years 1952 to 1976 there is no significant relationship between salmon catch during May and June and value of each crab delivery ($r = 0.31$).

DISCUSSION

Interpretation of the correlation functions computed here is somewhat subjective. Since, as described earlier, significance levels do not hold rigorously, they can be interpreted only in a relative sense. Correlations from the first-differenced data can supplement interpretations of the raw (except for detrending) data. First-differencing removes intraseries correlation, hence emphasizes changes between adjacent points in a series. Cross-correlations computed from first-differenced series are more sensitive to the timing of changes, and less sensitive to sustained high and low values. The lag between recurring changes in specific directions in each series must remain constant in order to produce a high cross-correlation. Significant correlations that do not remain high following first-differencing should not necessarily be regarded as spurious, rather they may stem from variables that are highly autocorrelated (e.g., abundance or catch as compared with age-class sizes). On the other hand significant correlations that remain high following first-differencing probably stem from variables with less intraseries correlation.

Computed cross- and auto-correlations support the existence of cyclic covariation between crab and salmon catch in northern California. The fact that the negative correlation at a lag of +2 (Fig. 3) is no longer significant after first-differencing (Table 1) implies that it probably arose from the extended periods of high constant crab catch and low constant salmon catch (Fig. 1).

These same characteristics appear to be present when each salmon species is considered individually. They are, however, weaker in the king salmon and weaker still in silver salmon. The shorter length of the silver salmon time series may be responsible for the latter.

The analysis of central California data is more informative, although it too is constrained by shorter series. Early catch records in central California resemble northern California records in some respects. The auto-correlations of both salmon and crab are the same and the cross-correlation function has the same general shape except that the peak at negative lag is at −3 yr and the peak at positive lag in northern California is at a lag of zero (Figs. 3, 7). This negative correlation at 0 lag is quite apparent in Figure 6. The most striking departure from the northern California situation is the substantial decline of the positive peak at negative lag and the persistence of the negative peak at 0 lag following first-differencing (Table 1). This implies that changes in crab and salmon that are in the same direction are less regular than changes in the opposite direction.

Following the decline in crab catch in central California the auto-correlation functions show weaker cycles of shorter period for the crab and the existence of a cyclic pattern for salmon is questionable. The cross-correlation function is similar to the predecline case but shifted to more negative lags. This could occur, for example, if two cyclic processes retained their shape but were shifted in time with respect to each other. After first-differencing the positive peak at negative lags persists yet the negative peak is diminished in magnitude by half. The postdecline period is similar to northern California in this respect but differs in having a negative correlation at a lag of −2.

The observed differences in lag value of points of significant correlation raise the question of whether the northern California crab or salmon fishery lags its central California counterpart. The cross-correlation between northern California and central California salmon catch for the period 1940 to 1976 has a significant positive

peak at +1 and +2 yr that remains significant at +1 yr after first-differencing. The same characteristics are present, though less strong, when the predecline and postdecline periods are considered individually. This lag of 1 or 2 yr between northern California and central California salmon catch is commensurate with the shift in the point of negative correlation for the predecline situation (Fig. 7). The cross-correlation between crab catches at the two locations does not show significant results nor do higher correlations persist after first-differencing.

We can consider the implications of observed correlations for three classes of possible mechanisms. The first class of mechanisms involves cyclic environmental factors which independently drive the cycles in each species. Differences in life history between the two species could be responsible for the phase difference between the two cyclic processes. In the second class of mechanisms, one species is cyclic because of environmental factors or an endogenous mechanism within the population and the second species is cyclic because of some linkage to the first species. The third possibility requires neither species to be inherently cyclic. Rather, a biological interaction between the two species results in cyclic behavior in both (e.g., as in a classical predator-prey system). The computed correlation functions place constraints on specific timing of the mechanisms in each of these classes. These can be compared with known life history characteristics and suspected interactions to eliminate some possibilities.

The life histories of the two species follow similar temporal patterns. The eggs of Dungeness crab and fall-run king salmon hatch in midwinter. The pelagic crab larvae drift for several months then settle as first crabs during April and May. The salmon fry remain in streams for several months then enter the ocean in late spring through summer. Some adult crabs enter the fishery 3 yr after hatching but most are caught at age 4. King salmon first enter the fishery about 2½ yr after hatching, and most are caught at 3½ yr and some are caught 4½ yr after hatching.

That there was no significant positive cross-correlation between the two catch records at 0 lag indicates that a cyclic environmental factor which drives the cycle of one species through an effect on one age-class cannot also affect the same age-class of the other species. This implies, for example, no direct interaction between the 0 age classes of the two species. This is to be expected since most crab larvae have settled before salmon smolts begin entering the nearshore pelagic environment.

The positive cross-correlation, which indicates that good (bad) salmon catches are followed 3 to 5 yr later by good (bad) crab catches, may be a result of a cyclic environmental factor which affects early salmon survival in 1 yr and similarly affects larval crab survival 3 to 5 yr later. This environmental factor need not affect exactly the same age class in both species. For example, a positive effect on growth and survival of maturing salmon in their penultimate year at sea and a simultaneous positive effect on ovary development in female crab could increase salmon catch in the following year and crab catch 4 to 6 yr later through increased egg production in the following year.

Salmon have been observed to prey heavily on pelagic crab megalopae (Orcutt 1978). If this mechanism is considered as increased larval crab mortality when salmon are abundant, it does not fit the conditions implied by the correlations. However, if abundant crab megalopae lead to a good crab year class while increasing the growth and survival of adult salmon, then the observed cross-correlation would result. A mechanism by which salmon were more available to the fishery during years of high crab larval abundance could also cause the observed covariation.

The negative cross-correlation indicates that good (bad) crab catches are followed 1 to 2 yr later by bad (good) salmon catches. That this does not persist following first-differencing is commensurate with it being a result of fluctuation in an auto-correlated series (e.g., abundance) rather than a less auto-correlated series (e.g., recruitment). The mechanism which is a priori the most likely cause of this observation was the one investigated in detail in this paper: the cycle in salmon catch is actually a cycle in fishing effort for salmon and that this cycle is driven by the highly cyclic crab catch.

The conclusion resulting from analyses of the hypothesis of behavioral switching by fishermen is that an immediate response to crab abundance is not a likely cause. The strongest evidence for this was the comparison of the cyclic nature of early with late season salmon catch. The other two analyses are less powerful because both the availability of salmon and the variation in weather conducive to salmon fishing introduce vari-

ability in April and May salmon catch. The conclusion drawn from the comparison of early versus late season catch, however, rests on observing the cyclic nature in the late season catch regardless of its cause.

While we have concluded that an immediate behavioral response is not a likely cause, other related possibilities remain. The observed covariation could be caused by an inherently cyclic crab fishery and a negative response of effort in salmon throughout the salmon season (rather than solely in the months of overlap). Further elucidation of the economic question awaits results of an ongoing study of microeconomic behavior of fishermen.

Consideration of the life histories of the species and the timing of events implied by the lags in correlation admits the possibility of direct interaction and dependence of both cycles on environmental factors. Oceanographic conditions have been suggested as causes of fluctuations in other fisheries. Wild (1980) recently proposed that a change in sea surface temperature in the late 1950's reflects a change in the marine environment that is responsible for the decline in the central California Dungeness crab fishery. He also suggested that changes in sea surface temperature were related to fluctuations in the northern California crab catch record. However the actual values of correlation between these processes are not significant. Southward et al. (1975) presented data on cyclic fluctuations in sea temperature and covarying changes in fish population parameters over the past 50 yr in the English Channel.

Though the observed changes in lags and sensitivity to first-differencing may not be related to the causal mechanism, the nature of the covariation between salmon and crab catch does appear to have changed following the decline in central California crab landings. This change is not explained by fishermen switching between species, but could stem from Wild's (1980) proposed change in oceanographic conditions. The decrease in the period of the cycles in crab abundance following the decline is of some interest with regard to the issue of the cause of the decline itself. One of the possible causes of a decrease in period of the cycles is an increase in individual growth rate. This increase in growth rate is a necessary component of one of the potential causes of the decline (Botsford 1981) but is difficult to demonstrate because of the paucity of samples before the decline.

Possible effects of internal population dynamics on the observed behavior are worthy of examination. An interage, density-dependent mechanism has been cited as a potential cause of the cycles in crab abundance (Botsford and Wickham 1978, 1979). A similar mechanism could be operating on salmon abundance if the several stocks in the fishery were in synchrony. Peterman (1978) found positive correlations in smolt-to-adult survivorship between several groups of Pacific salmon populations. Populations that are not density-dependent but reproduce only in their final year have also long been known to fluctuate in a cyclic fashion (Bernardelli 1941; Leslie 1945). However, the period of the cycles is equal to the age of reproduction rather than twice the mean age of reproduction as it is in the stock-dependent recruitment case (Ricker 1954; Botsford and Wickham 1978).

The methods used here could prove useful in other fisheries problems. While time-series techniques have been applied to fishery problems, the primary goal has been a final model of the fishery rather than a search for causal relationships. The latter approach, the one taken here, has the advantage of leading to models that are based on known causal mechanisms rather than correlations of unknown causal mechanisms. Since the nature of these mechanisms could change significantly (possibly because of a change in fishing policy itself), a policy that is cognizant of them will fare better than one that relies on a statistical description from the past.

Another analytical time-series technique that we have not used here is the computation of causality as defined by Granger (1969). His special definition of causality is based on whether addition of data from past time on one variable decreases the error with which another variable can be predicted. The investigations performed here are in the same spirit but do not result in a single quantitative measure of causality.

While we have demonstrated here a potentially important statistical relationship, we have not uncovered the underlying cause. The ultimate cause, however, is worth pursuing. Its discovery and quantitative description could put salmon and crab management on a firmer basis by supplying greater predictive ability. Management could then respond to abundance on a firmer, predictive basis rather than a trial-and-error basis.

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SWIMMING KINEMATICS OF SHARKS[1]

P. W. WEBB[2] AND RAYMOND S. KEYES[3]

ABSTRACT

Video-tape recordings were made of locomotor movements of six species of free-swimming sharks. The following kinematic parameters were measured, normalized where appropriate with total body length (L): tail-beat frequency (f), specific tail-beat amplitude (A/L), specific wavelength of the propulsive wave (λ/L), specific stride length (S/L), and the rate of change of A/L with position along the body. These parameters were measured over a range of swimming speeds up to 3.9 m/s (4 L/s) for one species, the blacktip shark, *Carcharhinus melanopterus*. Data were obtained only over a narrow range of low swimming speeds for the other species, because they could not be induced to swim at high speeds. For the blacktip shark, f increased with speed, but A/L, λ/L, and, hence, S/L all decreased as speed increased. Among the six species, λ/L and S/L tended to be larger for more fusiform species, while A/L and f, at a given speed, appeared to be lower. This implies swimming movements of more fusiform species generated more thrust per beat than elongate species and/or the swimming drag was lower. The pattern of amplitude changes along the body length of sharks was intermediate between that observed for elongate and fusiform teleosts.

Thrust and swimming efficiency can be improved when discrete fins interact, as between the dorsal and caudal fins of sharks. For this to occur, a phase difference of $\geq 0.5\,\pi$ must occur between the vortex wake shed at the trailing edge of an anterior fin and the leading edge motion of a more posterior fin, which interacts with the upstream vortex sheet. The variations in swimming kinematics with speed, the differences among the species studied, and the conservative nature of body form in sharks probably function to increase thrust and efficiency by such interaction between median fins.

Most studies on fish locomotion have concentrated on bony fish, especially teleosts. As a result, modern ideas on fish locomotor functional-morphology are dominated by knowledge of only one of the major groups of fish. However, there are many unique features among cartilaginous fish that suggest they have exploited some different biomechanical possibilities. Sharks appear to swim like elongate teleosts, but in contrast they have discrete, often widely spaced median fins more typical of fusiform teleosts. Lighthill (1970) and Sparenberg and Wiersma (1975) have shown that this combination provides an opportunity for median fins to interact in such a way that thrust and Froude efficiency (the ratio of useful work to total work of the propellor system) are improved.

If shark locomotion were to utilize flow interactions between median fins to hydromechanical advantage, they would have to swim somewhat differently from teleosts. For example, teleosts modulate tail-beat frequency with speed, but sharks might also have to vary other kinematic parameters, such as the length of the propulsive wave and tail-beat amplitude. Therefore, the following experiments were performed to determine how swimming kinematics and phase differences between fin motions varied with speed for six species of sharks. While difficulties were encountered in obtaining data over a wide range of speeds, the results suggest that sharks vary swimming kinematics to utilize interactions between median fins, as postulated by Lighthill (1970).

METHODS

Observations were made on six species of free-swimming sharks (Fig. 1). Three species, the bull shark, *Carcharhinus leucas*; lemon shark, *Negaprion brevirostris*; and nurse shark, *Ginglymostoma cirratum*, were approximately 2-2.5 m in total length. They were contained in the public display at Sea World, San Diego, Calif., described by Weihs et al. (1981). Specimens of the other three species were smaller; Pacific blacktip shark, *Carcharhinus melanopterus* (total length, $L = 0.97 \pm 0.5$ m; $\bar{X} \pm 2\text{SE}$; $N = 7$); bonnethead,

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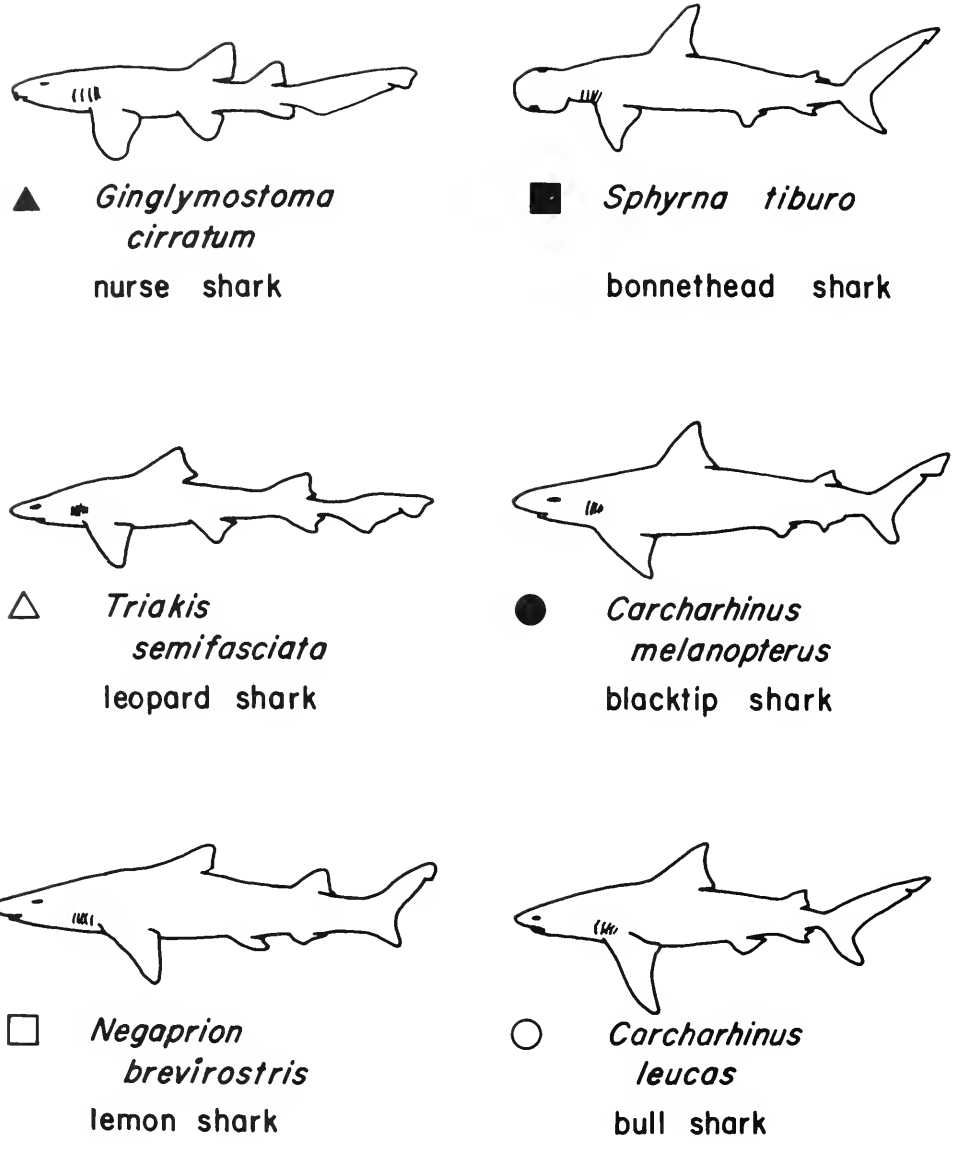

FIGURE 1.—Drawings (not to scale) showing the longitudinal body form of the six species of sharks for which swimming kinematic data were obtained. The symbols are used through most of the following figures.

Sphyrna tiburo ($L = 0.93 \pm 0.09$ m; $N = 5$); and leopard shark, *Triakis semifasciata* ($L = 0.98 \pm 0.11$ m; $N = 5$). The three smaller species were part of a second public display in an outside pool at Sea World. This pool was approximately oval in shape, 9 m long, 5.5 m wide, and 0.3 m deep. Small individual sharks were also observed in a small rectangular tank, 2.5 m long, 1.2 m wide, and 0.3 m deep. This tank had a transparent bottom. The water temperature in all three facilities was the same and constant at 24.5°C. Thomson and Simanek (1977) have shown that most sharks fall into one of four functional-morphology groups. Group 1 includes sharks with streamlined, fusiform, deep bodies; a narrow caudal peduncle with lateral flukes (streamlining); and a high aspect ratio tail. This group is represented by large pelagic species, such as *Lamna* which were unavailable for study. Group 2 is similar to group 1, but lacking the deep body and stream-

lined caudal peduncle. *Carcharhinus leucas*, *C. melanopterus*, and *S. tiburo* represent group 2. Group 3 includes sharks with a low aspect ratio tail, making a small angle to the horizontal, and a less fusiform body, represented by *G. cirratum*, *T. semifasciata*, and *N. brevirostris*. Group 4 incorporates the squaloid sharks, e.g., *Centrolepis*, which were not available.

Swimming movements were recorded on video tape. Recordings were made above the free surface of the public display facilities. Surface ripples were small compared with the images of the sharks and were therefore ignored. To avoid surface problems, observations in the rectangular tank were made from below through the transparent bottom. Surface ripples did not deleteriously affect measurement accuracy because no differences in data from the public facilities and the rectangular tank could be found.

Swimming records were obtained for as wide a range of speeds as possible. In most cases, normal variation in motor behavior due to the operation of the park was exploited. For the large sharks, observations were made before the display opened, during normal hours, and during feeding. Because of the possibility of injury leading to mortality, other invasive methods to induce higher speeds were not used. Similar procedures were employed for the smaller sharks. Underwater concussions, induced by dropping heavy objects (fluid-filled metal kegs), and visual stimuli were used to induce higher speeds in these sharks. Tactile stimuli were also employed to generate a range of speeds in the rectangular tank.

Video tape was analyzed "frame-by-frame," using manual advance to resolve movements to within 1/60 s (17 ms). Because a large length range was used, kinematic observations were normalized, for convenience, with respect to total length, L, measured from the tip of the nose to the tip of the tail. Specific swimming speed (speed/L), specific amplitude (amplitude/L), and tail-beat frequency (f) were measured for periods of steady swimming of two or more tail beats. The speed of the propulsive wave (c) was calculated from the backward displacement of wave crests, and specific wave-length (λ/L) was calculated from c/Lf.

RESULTS

Representative swimming movements for three of the species of sharks are illustrated in Figure 2. The body was bent into a wave that travelled backwards over the body at a speed greater than the swimming speed. The amplitude increased caudally to reach maximum values at the trailing edge (the tip of the caudal fin). In general, the form of propulsive movements was similar to that of other fish, as originally described by Gray (1933).

Kinematic parameters varied among the six species and with swimming speed. In practice, it proved extremely difficult to induce the sharks to swim over a wide speed range. This is consistent with experiences of Johnson (1970) with the brown shark, *Carcharhinus plumbeus* (= *C. milberti*), and Brett and Blackburn (1978) with the spiny dogfish, *Squalus acanthias*. Hunter and Zweifel (1971) reported kinematic data for a single leopard shark, *Triakis henlei*, swimming in a water tunnel, but the speed range is not given. Only the blacktip sharks swam over a speed range large enough to permit examination of the relationships between kinematics and speed. Data for the other species was therefore simply averaged (Table 1). The sharks also did not swim at very low speeds.

Tail-beat frequency increased linearly with speed (Fig. 3A), as found for other species of sharks and for teleosts (see Johnson 1970; Hunter and Zweifel 1971; Webb 1975; Aleyev 1977). However, frequencies increased at a higher rate with speed than observed for other fish. Mean specific speeds and tail-beat frequencies varied among the six species of sharks. Compared with the slope of the blacktip shark relationship, more elongate species (e.g., nurse shark; group 3 of Thomson and Simanek 1977) tended to have higher tail-beat frequencies at a given specific speed than more fusiform fish (e.g., bull shark; group 2 of Thomson and Simanek 1977) (Fig. 3B; Table 1).

Specific amplitude of the blacktip shark decreased with increasing speed (Fig. 3C) and hence was inversely related to tail-beat frequency. Specific amplitudes varied from 0.06 to 0.21 among species, with the more fusiform sharks having lower values (Fig. 3D). With the exception of the bull shark, mean specific swimming speeds were greater for the more fusiform species. Thus, for the interspecific data, specific amplitude decreased with specific speed, similar to the intraspecific observations on blacktip sharks. Among teleosts, both tail-beat amplitude and frequency may increase together at very low speeds (Bainbridge 1958; Webb 1971, 1973). However, over most of the speed range, caudal

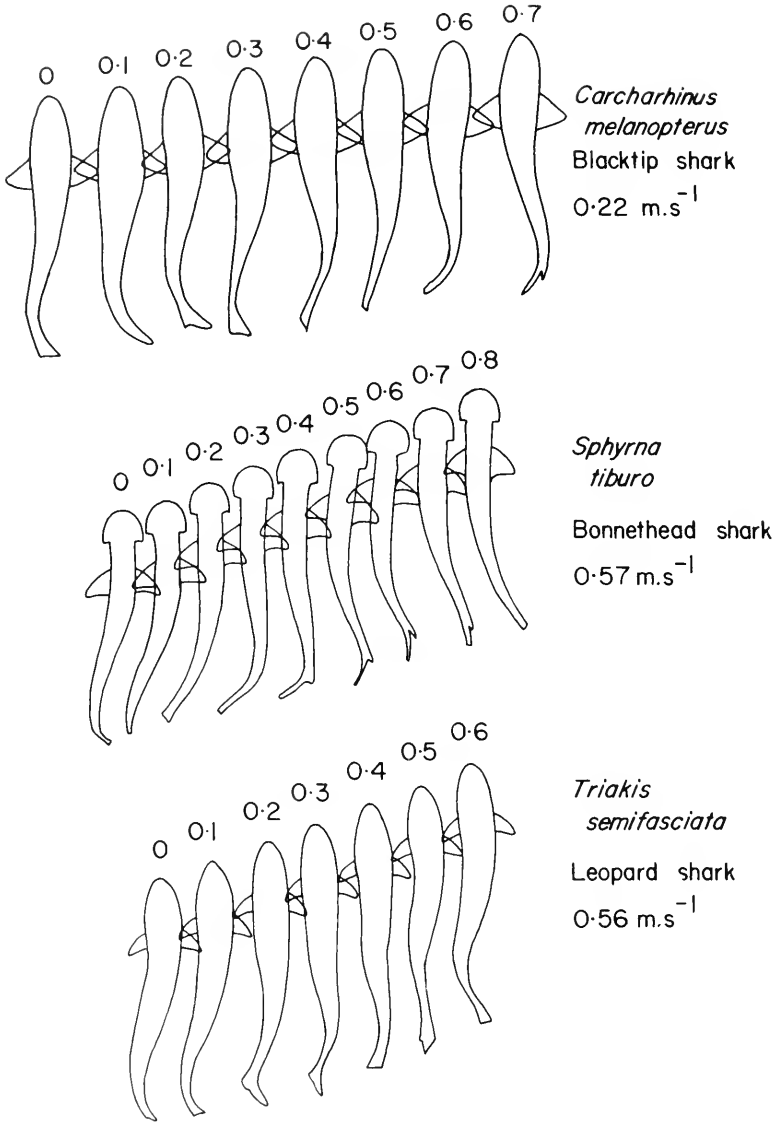

FIGURE 2.—Tracings from videotapes of three species of sharks swimming at three different speeds to show typical body movements. The times above each tracing are in seconds.

fin trailing edge amplitudes tend to be constant at about 0.2 L (see Hunter and Zweifel 1971).

In those cases where specific amplitudes and tail-beat frequencies have been related, their product (fA/L) is linearly related to speed. A similar relationship was calculated for this product using the relationships derived for *Triakis* by Hunter and Zweifel (1971) and was similar, but slightly curved for the blacktip shark (Fig. 3E). The product fA/L also increased with speed for the other species (Fig. 3F). The free-swimming sharks thus showed frequency and amplitude modulation with speed. This contrasts with *Triakis henlei* in a water tunnel where only tail-beat frequency was modulated, perhaps due to the presence of walls in the water tunnel. The modulation of both tail-beat frequency and amplitude with swimming speed explains the differences in the kinematics-swimming speed relationships between teleosts and sharks. It appears that the shark propulsive system is more plastic than that of bony fish.

Because of the interrelationships between tail-beat frequency, specific amplitude, and specific swimming speed, stride length also varied inversely with swimming speed for the blacktip

TABLE 1.—Summary of mean kinematic parameters for six species of sharks. Data show mean values ±2SE. Sharks are ranked according to their morphology from the most elongate to most fusiform species. This morphology would be expected to be associated with more anguilliform and more carangiform swimming, respectively.

Species	Specific swimming speed (U/L)	Tail-beat frequency (f, Hz)	Specific tail-beat amplitude (A/L)	$\frac{fA}{L}$	Specific stride length (S/L)	Specific wave-length (λ/L)	Phase difference (radians)	N
Nurse shark	0.34	0.67	0.21	0.15	0.51	—	—	12
	±0.04	±0.14	±0.04	±0.04	±0.08			
Leopard shark	0.58	1.12	0.20	0.22	0.55	0.77	0.53	10
	±0.15	±0.30	±0.04	±0.08	±0.10	±0.14	±0.18	
Lemon shark	0.47	0.95	0.18	0.16	0.58	—	—	6
	±0.14	±0.26	±0.06	±0.04	±0.09			
Bonnethead shark	0.84	1.25	0.18	0.23	0.64	0.91	0.46	14
	±0.11	±0.14	±0.02	±0.04	±0.03	±0.06	±0.08	
Blacktip shark	0.80	1.13	0.18	0.33	0.72	1.07	0.47	18
	±0.10	±0.14	±0.02	±0.12	±0.03	±0.09	±0.05	
Bull shark	0.58	0.78	0.16	0.13	0.74	—	—	5
	±0.09	±0.21	±0.03	±0.05	±0.14			

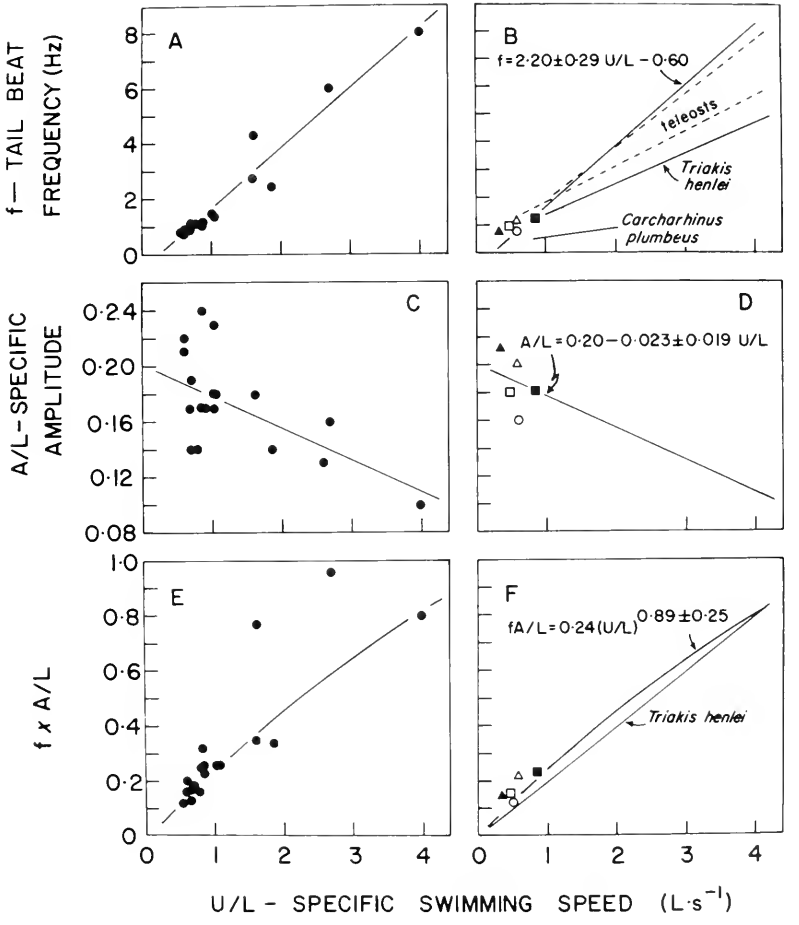

FIGURE 3.—Relationships between tail-beat frequency, f, specific amplitude, A/L, and their product, fA/L, as functions of specific swimming speed, U/L for various sharks. A, C, and E show data for blacktip sharks and best-fit functional regressions. These curves, and the pertinent equation, are shown with the mean values for the other species in B, D, and F. Values for the slope of the equations are the mean ±2SE. The key to symbols is in Figure 1. Other data are teleosts and *Triakis henlei* from Hunter and Zweifel (1971) and *Carcharhinus plumbeus* from Johnson (1970).

shark and among the six species (Fig. 4). Stride length is defined as the distance travelled per tail beat (Wardle 1975). In teleosts, specific stride length (stride length/L) typically takes values of 0.6 to 0.8, and does not vary with speed (Wardle 1975). In blacktip sharks, specific stride lengths comparable with those of teleosts were seen only at low speeds and stride length was lower at higher speeds. Specific stride length was similar to the teleost values in the more fusiform sharks, but was lower in more elongate species, the lowest value of 0.51 L being found for nurse sharks (Table 1, Fig. 4).

Data on specific wavelengths were only measured with sufficient accuracy for the three smaller species. Values ranged from 0.77 to 1.07 L, and tended to be larger for the more fusiform species. Specific wavelength decreased with specific swimming speed in blacktip sharks (Fig. 5), contrasting with teleosts, where specific wavelength is usually independent of speed (Webb 1971, 1973; Wardle and Videler 1980).

Rates of change in amplitude were measured along the body length. In the sharks, there was an area along the body, about 0.2 L from the nose, where both amplitude and its rate of change with body length were least (Fig. 6). Anterior to this area, rates of change in amplitude were negative where amplitude increased rostrally due to yawing of the nose. These patterns are similar to those of teleosts. The maximum rate of increase in amplitude in sharks occurred from 0.5 to 0.7 L, and declined over more posterior portions of the body. This particular pattern has not been described in teleosts, which usually show an early rise in amplitude (e.g., eel) or sustain increasing rates of amplitude over the whole caudal region (e.g., fusiform teleosts). The area over which amplitude begins to increase in sharks is close to the region of the trailing edge of the first dorsal fin (Thomson and Simanek 1977).

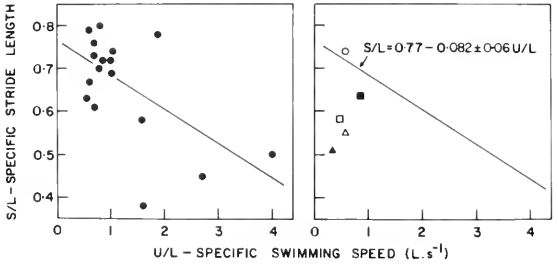

FIGURE 4.—The relationship between specific stride length, S/L, and specific swimming speed, U/L for several sharks. The key to symbols is in Figure 1.

DISCUSSION

The diversity of swimming kinematics in fish was originally described and classified by Breder

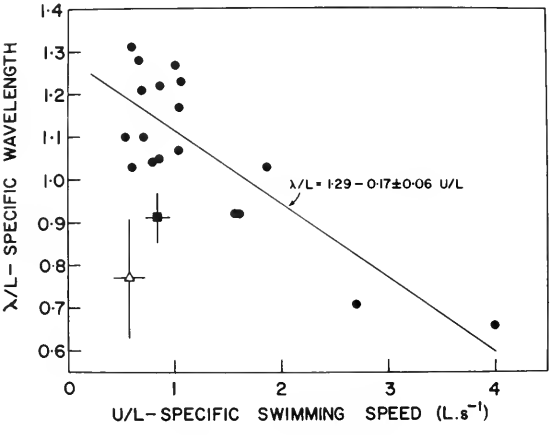

FIGURE 5.—The relationship between specific wavelength, λ/L and specific swimming speed, U/L for three species of shark. Vertical and horizontal bars are ±2SE. The functional regression was fitted only to data for the blacktip shark. The key to symbols is in Figure 1.

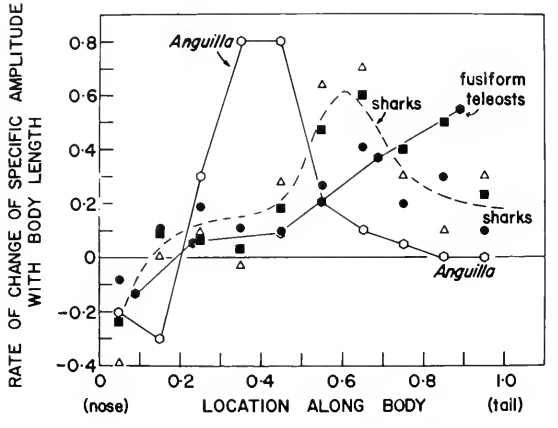

FIGURE 6.—The relationship between the rate of change of amplitude along the body length and the position along the body in some fishes. The data for fusiform teleosts (solid hexagons linked by solid lines) were taken from Bainbridge (1963) for dace, *Leuciscus leuciscus*, and bream, *Ambramis brama*. Data for Anguilla (open hexagons linked by a solid line) were taken from Gray (1933). Data for the sharks (see key in Fig. 1) were taken from Figure 2; the dotted line was fitted by eye through the data for sharks.

(1926), and has been more recently updated by Lindsey (1978). The definition of common locomotor patterns, or modes (Lighthill 1975), for undulatory swimming movements of the body and caudal fin are based on the number of one-half wavelengths contained within the body length and the pattern of increasing amplitude along the body. The elongate eel, *Anguilla*, is definitive for the anguilliform mode where the body contains more than one-half wavelength within the body length, and often one or more complete waves. The lateral amplitude of body movements rises early and is large over most of the body length. Jacks, in the family Carangidae, are representative of the carangiform mode where the body length contains less than one-half wavelength, and lateral displacements increase rapidly over the posterior third or half of the body. Breder (1927) used the term "sub-carangiform mode" for fish with wave patterns of the anguilliform mode and amplitude changes similar to the carangiform mode. So far, detailed studies of fusiform teleosts have been on subcarangiform swimmers.

The six species of shark are also subcarangiform swimmers according to these definitions; the body contained more than one-half of a wave (Table 1, Fig. 5) and the amplitude of body movements increased predominantly over the posterior half of the body (Fig. 6). However, the maximum rate of increase in amplitude occurred over the third quarter of the body, intermediate between the situation for elongate and fusiform teleosts. Therefore, although the sharks swam in the subcarangiform mode, they were more eel-like than fusiform teleosts. This is consistent with the unaided visual impressions of shark swimming.

Among teleosts, trends in swimming kinematics from the anguilliform mode towards carangiform modes are associated with changes in body form from an elongate, flexible body to a more fusiform, less flexible body. This is coupled with a larger caudal fin depth increasingly separated from the body by a narrow caudal peduncle, a morphology defined as narrow necking (Lighthill 1975). The same trends are seen in the six species of sharks studied here (Fig. 1, Table 1). The more fusiform species were those with longer propulsive wavelengths and a larger tail depth swimming in a more carangiform mode than the elongate sharks. In terms of the classification of shark functional morphology by Thomson and Simanek (1977), group 1 is most carangiform and groups 3 and 4 are most anguilliform. Group 1 representatives were not studied here.

The two factors of increasing wavelength and caudal fin depth in the carangiform swimmers are known to increase thrust and Froude efficiency (Lighthill 1975). However, thrust is reduced by a decrease in tail-beat amplitude. Among the sharks, increasing wavelength and tail depth were found with smaller amplitudes. Thus, the more fusiform, more carangiform species show features that would both enhance and decrease performance. Stride length increased in these more fusiform sharks so that overall the larger wavelength and deeper caudal fins must generate more than enough thrust, perhaps more efficiently, to offset reduced amplitudes.

The details of kinematic movements appear very different for sharks compared with bony fish. In the teleosts that have been studied to date (see Hunter and Zweifel 1971; Aleyev 1977) tail-beat frequency is the major kinematic variable with speed, and over most of the range of swimming speeds, it is the only variable. In contrast, the blacktip shark modulated all three of the kinematic variables that influence thrust: tail-beat frequency, tail-beat amplitude, and the length of the propulsive wave. Teleosts vary one morphological parameter with speed that would also affect thrust. This is the depth of the caudal fin trailing edge (Bainbridge 1963; Webb 1971) to vary the mass of water accelerated by propulsive movements (see Alexander 1968; Lighthill 1975). The skeleton of shark fins is based on cartilaginous ceratotrichia, rather than bony rays, which cannot be individually controlled. As a result, shark fins lack the flexibility to substantially modify fin depth during swimming.

The differences in locomotor kinematics with speed of the sharks illustrated by the blacktip shark, compared with teleosts, may be related to hydrodynamic interactions between the median dorsal fins and the caudal fin. This interaction was first described by Lighthill (1970) and has been developed in detail using hydromechanical theory for inviscid fluids by Sparenberg and Wiersma (1975). A vortex sheet is shed by the trailing edge of any sharp fin or body edge. This vortex sheet travels downstream, but it also has a lateral velocity component determined by the motion of the trailing edge; i.e., the wake follows a sinusoidal path (see illustrations in Rosen 1959; Aleyev 1977). The vortex sheet carries momentum determined by the motions and dimensions of the body and fin at the fin trailing edge.

The momentum carried in the vortex sheet will contribute to instantaneous thrust, and if there is no downstream fin to influence the flow, this momentum will contribute to the mean thrust and power of the fish (Wu 1971; Newman and Wu 1973). However, when there is a downstream re-entrant fin (i.e., a second downstream median fin spanning the flow from the anterior fin) the vortex sheet will impinge on the leading edge of that fin. If the gap between the fins is small, there is little difference between the motion of the incident vortex sheet and the motion of the leading edge of the downstream fin. Then the mean strength of the vortex sheet shed by the downstream fin is determined by the motion of that fin, with no significant contribution from the upstream vortex sheet from the anterior fin, i.e., the upstream fin has no effect on the wake eventually shed by the fish. In this case, the interaction between median fins does not influence mean thrust.

Lighthill (1970) showed that a different situation can occur when the gap between median fins is large. Under these circumstances, there may be a large enough phase difference between the motion of the incident vortex sheet and the downstream fin, so that the momentum shed upstream is not annihilated by the second fin. Then, the work done by the anterior fin against the momentum shed by its trailing edge together with that due to an increased incident velocity at the downstream fin increase total power output and improve efficiency (Lighthill 1975:80-84; Sparenberg and Wiersma 1975).

The phase difference in the motion of the trailing edge of one fin located at a position a_1, along the body, and the leading edge of a second more posterior fin at position a_2, is $2\pi(a_2 - a_1)/\lambda$ where λ is the length of the propulsive wave. However, the vortex sheet travels downstream at the mean speed, U, of the fish, while the body undulation travels backwards at a speed c, greater than U. Therefore, the phase difference, ϕ, in the motions of the vortex sheet shed by the anterior fin and the leading edge of a posterior fin is given by (Lighthill 1975, equation 28):

$$\phi = 2\pi\left(\frac{a_2 - a_1}{\lambda}\right)\left(\frac{c}{U} - 1\right). \qquad (1)$$

Sharks typically have three median fins, the first and second dorsal fins and the caudal fin. Thomson and Simanek (1977) have analyzed several morphological features of 56 species of sharks and show that the second dorsal fin is characteristically small compared with the first dorsal fin, especially in pelagic species. In addition, the second dorsal fin would only be partly re-entrant to most of the vortex sheet shed by the upstream fin because of the posterior taper of the body. Therefore, it seems likely that the second dorsal fin has relatively little effect on the flow between the other two fins during steady cruising. Thomson and Simanek's observations also indicate that the caudal fin depth is typically greater than or equal to that of the trailing edge of the first dorsal fin, as required to maximize the interaction. Therefore, ϕ was calculated for interactions between the first dorsal fin and the caudal fin of the blacktip, bonnethead, and leopard sharks (Table 2; Fig. 7). ϕ was close to, or $>0.5\pi$, as required for the interaction hypothesized by Lighthill (1970). A single record for the dogfish, *Acanthias vulgaris*, in Gray (1933) also gives a value of $\phi = 0.52\pi$ (Webb 1975). For

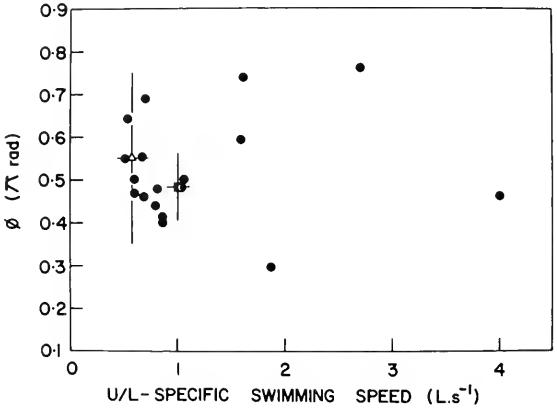

FIGURE 7.—The relationship between the phase difference ϕ (see Equation (1)) and specific swimming speed for three species of sharks. Vertical and horizontal bars are ±2SE. The key to symbols is in Figure 1.

TABLE 2.—Separation, $(a_2 - a_1)/L$, between the trailing edge of the first dorsal fin (a_1) and the mean position of the leading edge of the caudal fin (a_2), and phase difference (ϕ) between their movements for three species of sharks. ϕ was calculated from data in this table and in Figures 3 and 4 using Equation (1).

Species	$(a_2 - a_1)/L$	ϕ ($\bar{X}$±2SE) (π radians)
Leopard shark	0.48	0.55±0.20
Bonnethead shark	0.50	0.48±0.08
Blacktip shark	0.47	0.51±0.05

blacktip shark, ϕ was of the order of 0.5π over the range of swimming speeds studied.

In Equation (1), a_1 and a_2 are constants, and therefore, f or λ can be varied at any speed to keep $\phi \geq 0.5\pi$. However, such changes also affect thrust. For example, if λ varies with speed, compensatory changes in tail-beat frequency and/or tail-beat amplitude must occur to balance thrust and drag at a given speed. The blacktip shark modulated both. Therefore, the modulation of wavelength, amplitude, and frequency with speed can be explained in terms of mechanical advantages from an interaction between widely spaced median fins. It should also be noted that the early rate of increase of amplitude along the body in sharks, occurring near the first dorsal fin, might increase the strength of the vortex sheet. This could enhance thrust, perhaps more than would occur with patterns of increasing amplitude seen in fusiform teleosts.

Adaptive flow interactions between median fins as suggested by Lighthill (1970) apply to the established flow patterns of a steadily swimming fish. Therefore, the common body form and kinematic patterns of sharks appear to be adaptations for cruising. Some sharks, analogous in form to tuna (group 1 of Thomson and Simanek 1977), are obviously highly specialized for cruising (Lighthill 1975; Lindsey 1978), but the present observations suggest that other sharks are also specialized through the utilization of other principles, exploiting more anguilliform propulsion and a more elongate, flexible body. The distribution of the median fins along the body is very similar among sharks (Thomson and Simanek 1977). This suggests that such cruising adaptations are relatively common. Furthermore, sharks are frequently negatively buoyant, when continuous forward motion is important in swimming free from the bottom. This argues for the importance of cruising in the routine behavior of sharks, and hence the importance of any mechanisms to enhance thrust and efficiency in steady swimming.

Comparative observations on teleosts also suggest that in general, sharks are specialized in cruising. Experimental studies have shown that optimal design for transient swimming patterns (angular and linear acceleration) differs from, and is largely exclusive of, that for steady swimming such as cruising (see review by Webb in press). In teleosts, optimal morphological features for steady swimming include a small area anterior to a deep high aspect ratio tail propelling a fairly rigid body. For maximum acceleration, depth (and hence area) should be large over the whole length of a flexible body. Bony fish can achieve some compromise because of their flexible fins, but in general design for unsteady acceleration activity appears most important (Webb 1982). Compromises are excluded for sharks because they do not have collapsible fins. In addition, the separation of the median fins reduces the area of the body available to generate large forces for acceleration. Some sharks, e.g., the horn shark, *Heterodontus francisci*, have somewhat enlarged median fins that suggest a greater importance of acceleration. In general, a more posterior location of the first dorsal fin is associated with larger area fins, as in *Ginglymostoma cirratum* that could similarly improve acceleration. In this case the more posterior location of the first dorsal fin may be at the cost of reducing ϕ below 0.5π. However, the body and fin form typical of sharks (Thomson and Simanek 1977) probably provides for poor acceleration performance.

In conclusion, sharks appear to have exploited their different structural capacities to specialize for cruising when swimming.

ACKNOWLEDGMENTS

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POPULATION BIOLOGY OF CHUM SALMON, *ONCORHYNCHUS KETA*, FROM THE FRASER RIVER, BRITISH COLUMBIA

TERRY D. BEACHAM[1] AND PAUL STARR[2]

ABSTRACT

Population biology of Fraser River chum salmon, *Oncorhynchus keta*, was investigated. Mean age of chum salmon during the run declined from 3.98 years in October to 3.78 years in December in the 1970s. Females were more abundant than males in 4-year-old chum salmon, but males were more abundant than females in 3- and 5-year-old chum salmon. Fecundity of females was 3,250 eggs/female at a standard length of 58.0 cm and did not vary among years sampled. Fry tended to migrate downstream earlier when the previous winter had been warm than when it was cold. Egg-to-fry survival was correlated with rainfall, air temperature, and number of eggs deposited. Mean age of return of a brood year was positively correlated with its abundance. The return to escapement ratio for even-numbered brood years was inversely correlated with the abundance (catch plus escapement) of the previous brood year, which suggests that marine survival of chum salmon may be density-dependent. The return to escapement ratio for odd-numbered brood years was positively correlated with early downstream migration of chum salmon fry relative to pink salmon, *O. gorbuscha*, fry and with increased chum salmon spawning escapements relative to those of pink salmon.

Stocks of chum salmon, *Oncorhynchus keta*, in British Columbia and Alaska have fluctuated considerably in abundance (Hoar 1951; Wickett 1958; Hunter 1959; Helle 1979). These fluctuations have been attributable to variability in freshwater and marine survival, and have been related to climatic factors such as rainfall (Wickett 1958) and to population density or predation on fry (Hunter 1959). Chum salmon in British Columbia return to spawn in their natal streams mainly as 3- and 4-yr-olds, and to a lesser extent as 5-yr-olds. The mean age of returning adults tends to be greater for stocks from northern British Columbia than from southern British Columbia (Pritchard 1943; Ricker 1980). Chum salmon tend to spawn later in the fall than other species of *Oncorhynchus*, and the fry migrate downstream in the spring, within a few days after emerging from spawning beds.

The chum salmon stocks of the Fraser River have supported commercial fisheries in Johnstone Strait, the Strait of Georgia, and the Fraser River for many years (Palmer 1972) (Fig. 1). Annual catches of chum salmon were extensive in Johnstone Strait during 1951-54, ranging from 0.7 to 2.0 million fish, and in the Fraser River, ranging from 274,000 to 479,000 fish. However, the annual contribution of Fraser River chum salmon to the Johnstone Strait catch is unknown before 1964. Catches of chum salmon declined substantially during 1965-69, ranging from 23,000 to 649,000 fish in Johnstone Strait (an estimated 0 to 228,000 Fraser River chums), and 10,000 to 196,000 fish in the Fraser River. Catches have continued to vary widely in the 1970s. Fraser River chum salmon have thus shown marked fluctuations in abundance, and these fluctuations have not been satisfactorily accounted for. It is not currently possible to identify stocks of Fraser River chum salmon, so for purposes of the analysis, Fraser chum salmon were treated as a unit stock. This paper describes the population biology of Fraser River chum salmon and results of studies on the causes of variability in the number of returning adults.

MATERIALS AND METHODS

Estimates of abundance of returning adult and downstream migrating fry were derived by different sampling methods. Fry were enumerated during 1965-81 on the lower Fraser River near Mission City (Fig. 1) using techniques previously described by Todd (1966) and Bailey

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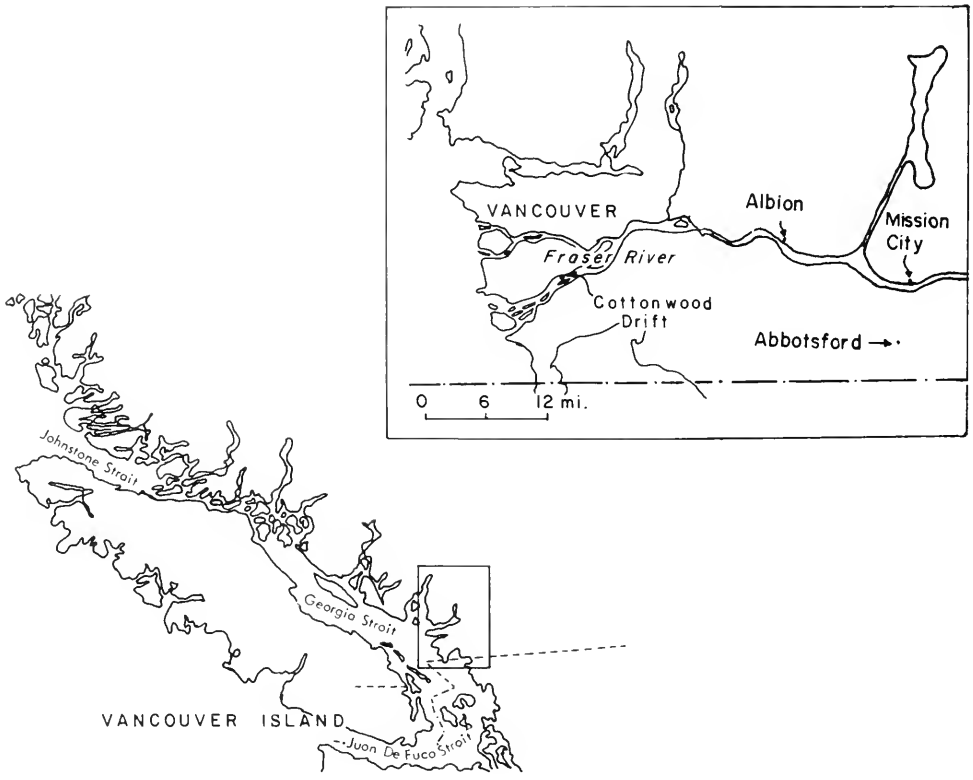

FIGURE 1.—Areas in British Columbia where Fraser River chum salmon are caught in the commercial fishery. Inset shows areas in the lower Fraser River where fry and returning adults were sampled.

(1979[3]). Briefly, the sampling procedure consisted of suspending traps at various depths from the surface to 3.7 m (12 ft) from either side of a boat travelling at a constant velocity relative to the water for 15-min periods. Samples were taken in this manner between 0500 and 1300 h. Preliminary sampling had established that chum fry migrated past Mission City were most active during this period. Sampling occurred during this period, 5 d a week from beginning of March to end of May. Daily sampling was continued for 24 h 2 or 3 d/wk so that estimates of the daily proportion of fry migrating during the standard shift (0500 to 1300 h) could be made, and daily totals of chum fry migrating past Mission City calculated. Sampling was also performed at different sites across the 527 m (1,725 ft) width of the Fraser River at Mission City. The depth and cross-sectional area of the river were known at each sampling site, as well as the area sampled by the fry traps, so that, by extrapolation, the number of fry migrating downstream daily could be estimated. Abundance of chum salmon fry used in the present analysis was taken from Bailey (footnote 3), as were the dates when 50% of the chum and pink, *O. gorbuscha*, salmon fry were estimated to have migrated past the sampling site. Weekly mean lengths (mm) of fry were determined in 1978.

Sex ratios, age composition, length-at-age, and fecundity of adult chum salmon arriving at the river mouth were derived from test fishing conducted at Cottonwood Drift from 1962 to 1979 and Albion from 1978 to 1979 (Fig. 1). A 274 m (150-fathom) long, 60-mesh deep gill net having 16.9 cm (6¾ in) mesh was set for a standard 30-min drift twice a day during the slack period of the lowest tide of the day. Smaller fish may have avoided capture on account of gill net selectivity (McCombie and Berst 1969; Todd and Larkin

[3]Bailey, M. D. 1979. Enumeration of salmon in the Fraser River. Unpubl. manuscr., 122 p. Department of Fisheries and Oceans.

1971), which could possibly bias adult age composition, sex ratios, and fecundity estimates. However, we believe that any bias present was not of sufficient magnitude to mask trends in abundance of individual brood years. Daily test fishing 5 d/wk was usually conducted from late September until mid-December, although sampling within this period was not conducted when the commercial fishery was operating in the river. Ages of chum salmon were determined from scales. Bilton and Ricker (1965) and LaLanne and Safsten (1969) have outlined the methodology of using scales for aging chum salmon. Lengths were recorded as either fork length or postorbital-hypural length to the nearest millimeter. Fecundity was determined by direct counts of the number of eggs in both ovaries. Age composition in the escapement was assumed to be the same as that in the test fishery. Escapement was estimated during the 1960s by visual counts on spawning beds, by test fishing, and by a tagging program (Palmer 1972), whereas in the 1970s, escapement was estimated from visual counts and test fishing only. Total returns for a brood year included the catch plus escapement.

Fraser River chum salmon are taken by the fishery which operates near the river mouth, and by fisheries in Johnstone Strait, the Strait of Georgia, and at Point Roberts in the United States. The proportion of Fraser River chum salmon in the Johnstone Strait fishery was estimated seasonally based on the tagging studies reported by Palmer (1972). Since the fishery in the Strait of Georgia exploits mixed stocks of chum salmon, it was not possible to estimate the contribution of Fraser River chum salmon in this fishery, although it is small compared with the catch in Johnstone Strait. Catches in the Fraser River, as well as 100% of the catches off Point Roberts, and the Fraser River contribution to Johnstone Strait were summed to estimate the total annual catch of Fraser River chum salmon. Although not all chum salmon caught off Point Roberts, 20 km south of the Fraser River mouth, may be bound for the Fraser River, any overestimation of the Fraser River contribution to the Point Roberts catch is compensated for by underestimation of the Fraser River contribution to the Strait of Georgia catch. Escapements of pink salmon used in the present study were those listed in the annual report of the International Pacific Salmon Fisheries Commission for 1979 (Anonymous 1980).

RESULTS

Marine Growth

High-seas scale and tagging studies have indicated that chum salmon from British Columbia and Alaska range from lat. 45°N to 60°N and from long. 130°W to 180° in the North Pacific Ocean (Shepard et al. 1968). Specific distributions of Fraser River chum salmon were not available. However, the effect of variability in ocean water temperatures on growth rate was investigated by comparing the mean monthly temperature from March through August (major part of growing season) at Station P (lat. 50°N, long. 145°W) and mean length-at-age of returning adults. Fork lengths of returning adults during 1960-69 were taken from Palmer (1972) and were converted to postorbital-hypural lengths by the regressions:

$$\text{Males: } H = 1.08\,FL - 219\ (N = 100,\ r = 0.72)$$
$$\text{Females: } H = 1.00\,FL - 130\ (N = 100,\ r = 0.89)$$

where FL = fork length in millimeters and H = postorbital-hypural length in millimeters. These regressions were derived from chum salmon taken by the Fraser River commercial fishery in 1962 and 1963. Postorbital-hypural lengths of returning adults during 1970-78 were derived from the test fishery at Cottonwood Drift. For the period of 1960-78, mean lengths-at-age of 4-yr-old chum salmon were correlated with water temperature at Station P during the penultimate growing season for males ($r = 0.49$, $n = 19$, $P<0.05$) and females ($r = 0.44$, $n = 19$, $P<0.06$). However, there was no correlation for mean length-at-age and water temperature at Station P during the penultimate growing season for age-3 fish (males: $r = 0.17$, $n = 19$, $P>0.10$; females: $r = -0.08$, $n = 19$, $P>0.10$) or in the year of return and mean length-at-age for age-3 fish (males: $r = 0.17$, $P>0.10$; females: $r = 0.10$, $P>0.10$). The relatively stable mean length-at-age for returning age-3 chum salmon is undoubtedly due to selectivity of the sampling gear, with possibly only the larger age-3 fish susceptible to capture in a 16.9 cm mesh gill net.

Age Composition and Sex Ratios of Returning Adults

The mean monthly age composition of chum salmon migrating upstream during the years

1970-79 indicated that the proportion of age-5 fish in the run decreased from October through December, whereas the proportion of age-3 fish increased (Table 1). Age-4 chum salmon comprised about 74% of the run in each month, while age-3 comprised 24% of the run in December but only 14% in October.

Sex ratios were variable among ages, with more male chum salmon returning at age 3 (X^2 = 23.7, df = 1, $P<0.01$) and age 5 (X^2 = 10.7, $P<0.01$) than did females (Table 2). More female chum salmon returned at age 4 than did males ($X^2 = 70.6$, $P<0.01$). Since the mean age of chum salmon in the run decreased through time, and sex ratios vary with age, the sex ratio of the run may also vary through time. However, an application of the sex ratios by age in Table 2 to the age compositions in Table 1 shows that sex ratios of the total run were nearly the same each month (52.9% females in October, 53.1% in November, and 52.9% in December).

TABLE 1.—Percentage age composition by month (October-December) of chum salmon sampled in the Fraser River test fishery, 1970-79. Sample sizes are in parentheses.

Age	October	November	December
3	13.7 (326)	21.7 (715)	23.8 (307)
4	74.3 (1,826)	74.3 (2,443)	73.4 (947)
5	12.0 (304)	4.0 (132)	2.6 (36)
Total	100.0 (2,456)	100.0 (3,290)	100.0 (1,290)
Mean age (yr)	3.98	3.82	3.78

TABLE 2.—Sex ratios (males:females) of age-3, -4, and -5 chum salmon sampled in the Fraser River test fishery, 1960-79.

Age:	3	4	5
Ratio	1.19	0.79	1.30
Sample size	3,172	5,378	626

Fecundity

Fecundity was determined from samples of chum salmon taken in 1966, 1968, and 1978 with females ranging in postorbital-hypural length from 50 to 66 cm. Females sampled in 1978 were generally larger than those in 1966 and 1968 (Table 3). A two-way analysis of covariance with sampling year and age as factors and length as a co-variate (co-variate was accounted for before factors were tested) indicated that there was no significant difference in fecundity (F) among years ($F=0.92$, df = 2 and 228, $P>0.05$) or among ages ($F = 2.66$, $P>0.05$). The mean fecundity for all samples was 3,250 eggs/female (Table 3).

The relationship between fecundity and length of 234 females sampled was described by:

$$\log_e F = 2.8659 + 0.8193 \log_e L \; (r = 0.29) \quad (1)$$

where F = fecundity and L = postorbital-hypural length in millimeters. The regression was significant ($F = 20.1$, $P<0.01$), but accounted for about only 9% of the variability in fecundity (Fig. 2). Most of the females sampled were between 54 and 63 cm in length, and with high variability in fecundity within this short length range, little of the variability in fecundity could be accounted for by the regression.

TABLE 3.—Number of females sampled, mean length (cm), mean age (yr), and mean fecundity of chum salmon from the Fraser River. SE = standard error of mean.

Year:	1966	1968	1978	Total
n	109	76	49	234
Length	57.4	57.9	59.5	58.0
SE of length	0.2	0.3	0.4	0.2
Age	3.90	3.89	3.90	3.90
Fecundity	3,227	3,276	3,261	3,250
SE of fecundity	39.5	46.6	60.1	27.7
Age:	**3**	**4**	**5**	
n	26	194	2	
Length	55.8	58.1	58.3	
SE of length	0.6	0.2	1.3	
Fecundity	3,292	3,246	3,091	
SE of fecundity	83.6	28.4	287.9	

Fry Migrations and Survival

The major portion of the downstream migration of chum salmon fry passed the Mission City sampling site from mid-March to the end of April. Usually 50% of the fry had passed the sampling site between April 13th and the 23d (Fig. 3), although 50% of the fry have passed the sampling site as early as April 3 (1976 brood year) and as late as May 3 (1971 brood year). About 80% of the chum salmon fry migrate downstream at a length of <40 mm. However, the proportion of fry >40 mm long during the downstream migration tends to increase with time. By the second week of May 1978, 20% of the fry were >43 mm long and weighed 1.0 g, which suggests a period of freshwater rearing for these fry.

Linear regression was used to determine the relationship of air temperature (T), determined as the mean of monthly air temperatures at the Abbotsford airport from December through February, to timing of the fry migration (F),

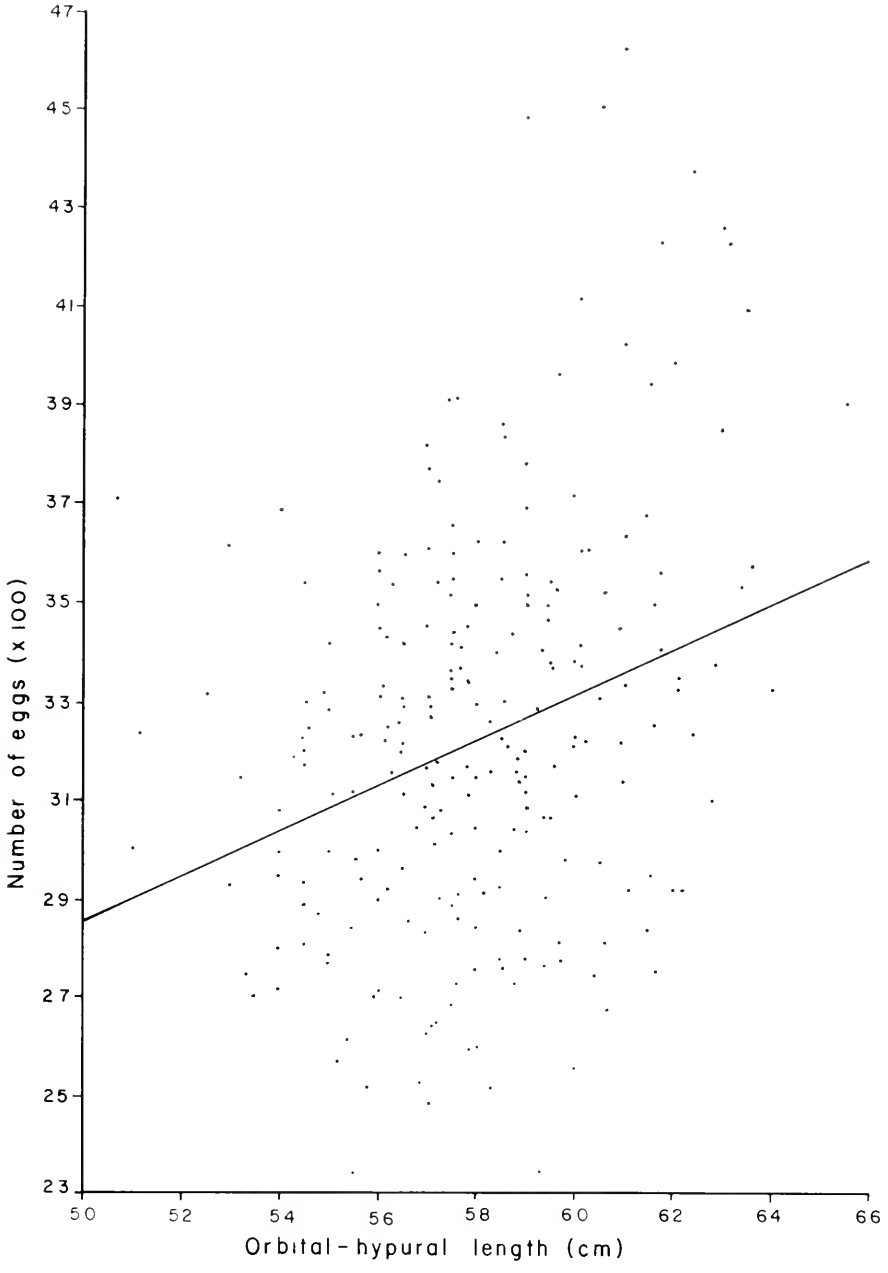

FIGURE 2.—The relationship between fecundity and length in female chum salmon sampled from the test fishery in 1966, 1968, and 1978.

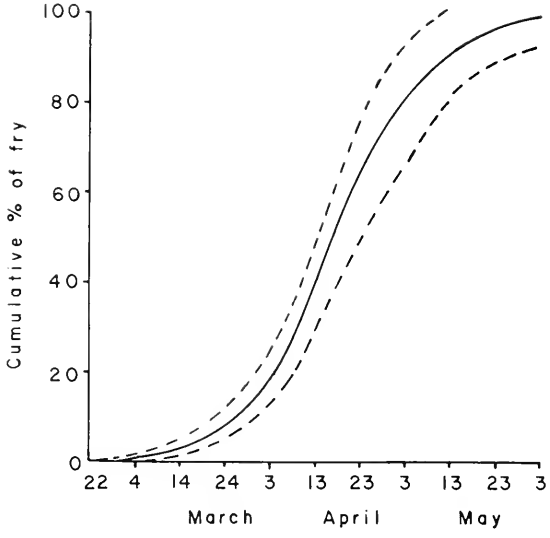

FIGURE 3.—Mean time of chum fry downstream migrations on the Fraser River, 1965-80. Dotted lines indicate 95% confidence limits.

measured as the days from April 1 to the date of 50% migration. Abbotsford airport is located near many major chum salmon spawning areas (Fig. 1). The model fitted was:

$$F = \frac{25.53}{T^{0.444}} \quad (n = 15) \qquad (2)$$

and the regression was significant ($r = 0.61$, $P<0.05$) (Fig. 4). Fry tend to migrate downstream earlier following a warmer winter than following a colder winter, presumably because warmer temperatures accelerate egg development.

Based on estimates of the number of migrating fry and egg deposition (Table 4), egg-to-fry survival varied from 6% to about 35% in the 1961-78 brood years. Multiple regression was used to determine the relationship of rainfall, egg numbers, air temperature, and their interactions on variability in egg survival. The model fitted through stepwise regression was:

$$S = a\ T + b\ T \times \frac{1}{R} + c\ T \times \frac{1}{E} + d\ T \times \frac{1}{R} \times \frac{1}{E} + e \qquad (3)$$

where S = % egg to fry survival

T = mean monthly air temperature at Abbotsford airport from December through February

R = total rainfall in cm at Abbotsford airport from November through January

E = number of eggs deposited $\times 10^6$.

The analysis yielded:

Variable	*Coefficient*	*SE*	*t*
T	−7.62	2.51	−3.03
T/R	615.90	130.42	4.72
T/E	4,369.52	1,375.07	3.18
T/RE	−266,517.54	77,530.32	−3.44
Constant	5.99		

The regression was significant ($R^2 = 0.77$, $F = 10.75$, df = 4 and 13, $P<0.01$), and the correlation matrix for the model is shown in Table 5. The individual factors of rainfall ($r = -0.28$) and egg numbers ($r = -0.005$) were not significantly correlated with egg survival, but their interactions with temperature were. Egg survival tended to increase during drier winters, but if these drier winters were also relatively cold, then egg survival was lowered. If the winter was both relatively dry and warm, then egg survival was good, as was the case for the 1976 brood year (Table 4).

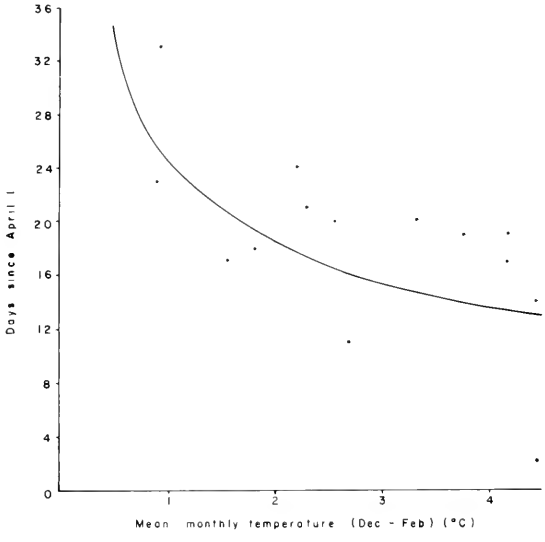

FIGURE 4.—Median date of downstream chum fry migration versus mean monthly temperature from December through February as measured at the Abbotsford airport.

TABLE 4.—Escapements, survivals, returns-at-age, mean age of return, and return to escapement ratios of Fraser River chum salmon, 1961-74 brood year. Percentage age composition for each brood year is in parentheses.

Brood year	Spawning escapement	No. of females	Egg deposition ($\times 10^6$) at 3,250/female	No. of fry ($\times 10^6$)	% egg to fry survival	Adult returns ($\times 10^3$)	% fry to adult survival	Return at age ($\times 10^3$) 3 yr	4 yr	5 yr	Mean age of return (yr)	Total return ($\times 10^3$)	Return to escapement
1961	164,000	83,800	272.4	25.8	9.5	236.3	0.91	98.6 (41.7)	132.0 (55.9)	5.7 (2.4)	3.61	236.3	1.44
1962	180,000	90,000	292.5	42.5	14.5	468.1	1.10	63.4 (13.5)	396.5 (84.7)	8.2 (1.8)	3.88	468.1	2.60
1963	214,000	107,000	347.8	54.8	15.8	178.2	0.33	50.7 (28.5)	123.6 (69.4)	3.9 (2.1)	3.74	178.2	0.83
1964	325,000	135,850	441.5	53.6	12.1	1,293.9	2.41	171.2 (13.2)	1,108.7 (85.7)	14.0 (1.1)	3.88	1,293.9	3.98
1965	185,000	109,930	357.3	32.4	9.1	579.8	1.79	211.9 (36.6)	363.9 (62.7)	4.0 (0.7)	3.64	579.8	3.13
1966	430,000	236,500	768.6	75.2	9.8	925.8	1.23	257.3 (27.8)	627.0 (67.7)	41.5 (4.5)	3.77	925.8	2.15
1967	212,000	102,600	333.5	69.0	20.7	325.4	0.47	53.5 (16.4)	224.5 (69.0)	47.4 (14.6)	3.98	325.4	1.53
1968	822,000	392,910	1,277.0	72.5	5.7	1,933.9	2.67	146.0 (7.6)	1,549.9 (80.1)	238.0 (12.3)	4.05	1,933.9	2.35
1969	390,100	206,360	670.7	107.4	16.0	1,434.6	1.34	58.5 (4.1)	1,174.4 (81.9)	201.7 (14.0)	4.10	1,434.6	3.68
1970	303,100	175,500	570.4	48.7	8.5	534.2	1.10	47.9 (9.0)	477.7 (89.4)	8.6 (1.6)	3.93	534.2	1.76
1971	356,700	142,980	464.7	58.2	12.5	367.7	0.63	161.0 (43.8)	200.7 (54.6)	6.0 (1.6)	3.58	367.7	1.01
1972	579,700	333,330	1,083.3	109.5	10.1	1,239.1	1.13	242.8 (19.6)	984.4 (79.4)	11.9 (1.0)	3.82	1,239.1	2.14
1973	453,000	250,510	814.2	130.8	16.1	653.0	0.50	205.7 (31.5)	427.5 (65.5)	19.8 (3.0)	3.72	653.0	1.42
1974	565,300	291,130	946.2	114.4	12.1	1,210.5	1.06	136.7 (11.3)	1,022.6 (84.5)	51.2 (4.2)	3.93	1,210.5	2.16
1975	235,300	125,990	409.1	73.0	17.8			158.9	227.4				
1976	588,700	310,830	1,010.2	358.2	35.4			96.7					
1977	538,800	271,020	880.8	124.3	14.1								
1978	486,600	268,603	873.0	88.1	10.1								
1979	327,700	173,700	564.5	109.4	19.4								

TABLE 5.—Correlation matrix for the egg-to-fry survival model. Variables are listed in the text.

	Variable				
	S	T	T/R	T/E	$T/E \times R$
S	1.00	0.52	0.73	0.22	0.29
T		1.00	0.80	0.66	0.60
T/R			1.00	0.49	0.64
T/E				1.00	0.93
$T/E \times R$					1.00

There was a slight tendency for egg survival to decline with increasing numbers of eggs deposited and this effect was enhanced by a cold winter. Thus spawning escapement (egg deposition), rainfall, and temperature interact to produce variable freshwater survival. Fry-to-adult survival was inversely correlated with egg-to-fry survival ($r = -0.62$, $n = 14$, $P<0.05$), which suggests a density-dependent response of chum salmon fry survival.

Age of Return

Total returns from the 1961 through the 1974 chum salmon brood years have ranged from 180,000 to 1,930,000 fish (Table 4). The proportion of the brood year returning at age 3 has ranged from 4% to about 42%. To determine if the mean age at maturity from a brood year was dependent upon the total number of adults produced from that brood year, we regressed mean age at maturity (in years) on total return (Fig. 5). This regression produced:

$$\text{Mean age} = 3.67 + 1.923 \times 10^{-7}\ \text{Returns} \qquad (n = 14) \quad (4)$$

where $r = 0.63$ ($P<0.05$). The mean age at maturity of a brood year increased as did the total num-

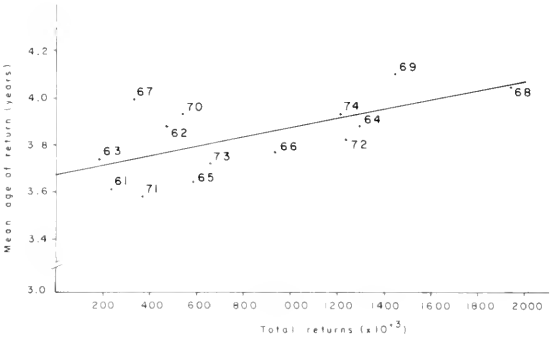

FIGURE 5.—Mean age of return of a brood year of chum salmon versus its abundance.

ber of returning adults, which suggests that if the timing of returns is size dependent, then density-dependent growth may occur during the ocean residence of chum salmon. Pink salmon return to the Fraser River in abundance in odd years, but return in negligible amounts in even years. The mean age at maturity and number of returning chum salmon adults tended to be higher in even brood years than in odd ones (Fig. 5), so that pink salmon may indirectly influence mean age at maturity of chum salmon through an effect on survival of chum salmon.

The proportion of a brood year returning at age 3, 4, and 5 is frequently of importance in predicting annual returns. For Fraser River chum salmon, the percentage age composition of the returns from a brood year is related to the mean age of return of the brood year as follows:

$$\% \text{ age } 3 = 321.56 - 78.26 \text{ mean age} \quad (r^2 = 0.93) \quad (5)$$

$$\% \text{ age } 4 = -141.68 + 56.20 \text{ mean age} \quad (r^2 = 0.63) \quad (6)$$

$$\% \text{ age } 5 = -79.88 + 22.06 \text{ mean age} \quad (r^2 = 0.50). \quad (7)$$

If the returns from a brood year can be predicted, then the mean age of return of a brood year can be obtained from Equation (4) and applied to Equations (5)-(7) in order to obtain numbers returning at each age.

Return to Escapement

The ratio of total returns for a brood year to escapement (R/S) has varied from 0.8 to 4.0 for the 1961 through 1974 brood years. The available evidence suggests that for escapements below 850,000 adults, egg-to-fry and fry-to-adult survivals will generally be large enough to allow the number of returning chum salmon to remain above replacement levels (Fig. 6). However, only the 1968 escapement was above 600,000 adults, so further information on the R/S ratio for escapements >500,000 adults is required in order to evaluate the effect of varying escapements on chum salmon survival. There was no evidence to indicate a decline in recruits per spawner at escapements >500,000 fish, and thus the optimal escapement is uncertain. Optimal escapements will not be established with confidence until declines in recruits per spawner (or density-dependent mortality) is observed at high spawning stock sizes.

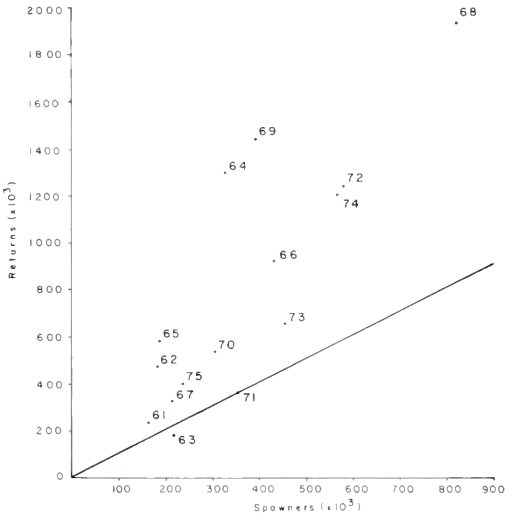

FIGURE 6.—Total return versus numbers of spawners for the 1961-75 brood years of Fraser River chum salmon.

Fry-to-adult survival has been variable, ranging from 0.3% to 2.4% (Table 4). The average survival for the even brood years was 1.53%, whereas survival for the odd brood years was 0.85%. The effect of fry abundance on variability in fry-to-adult survival was investigated for odd brood years by summing the estimated numbers of chum salmon and pink salmon fry, and for even brood years by assuming that the number of pink salmon fry produced was negligible. The data suggested that chum salmon fry survival tended to increase when the abundance of chum and pink salmon fry decreased (Fig. 7). This relationship can be expressed by:

$$\% \text{ survival} = 0.73 + \frac{46.53}{\text{Fry abundance (millions)}} \quad (r = 0.52) \quad (8)$$

for the 1961-75 brood years. All of the fry-to-adult survivals for the odd brood years, except for the 1965 and 1969 brood years, were below 1.0%, whereas all of the fry-to-adult survivals for the even brood years were above 1.0%, with the 1964 and 1968 brood year fry survival being higher than the rest.

Some of the variability in fry-to-adult survival was due to the timing of the downstream fry migration. The higher survival of the 1965 and 1969 brood year fry when compared with other odd

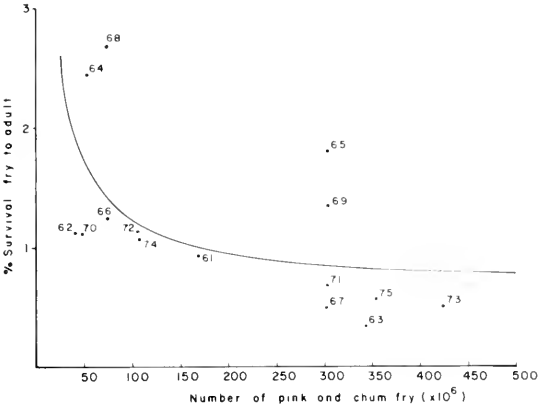

FIGURE 7.—Fry-to-adult survival for chum salmon versus total abundance of pink and chum salmon fry. The abundance of pink fry from even-numbered brood years was assumed to be negligible.

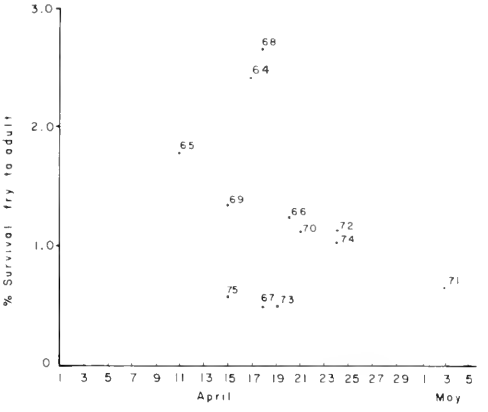

FIGURE 8.—Fry-to-adult survival of chum salmon versus median date of downstream migration.

brood years may be accounted for by the early downstream migration, and the same condition may apply to even brood years (Fig. 8).

With fry-to-adult survivals of Fraser River chum salmon generally lower in odd brood years than in even ones, odd- and even-numbered brood years were separated in a further analysis of variability in the returns to spawners relationship. The R/S ratio for even brood years was inversely related with the total number of returning adults of the previous odd brood year (Fig. 9). This relationship was determined through regression and is described by:

$$\frac{R_t}{S_t} = 1.367 + \frac{0.3867}{R_{t-1}} \quad (n = 7) \qquad (9)$$

where R_t = total returns for even-numbered brood year
S_t = spawning escapement producing that brood year
R_{t-1} = total returns of previous brood year in millions

and the correlation between R_t/S_t and $1/R_{t-1}$ was significant ($r = 0.91$, $P<0.01$). This equation can be rearranged to give a prediction of total number of returning adults in year t, given escapement and total return of the previous brood year. The above suggests that survival of chum salmon in the marine environment is dependent upon the abundance of conspecifics in the previous brood year. Marine survival may thus be density-dependent, and interbrood year interactions, possibly through competition for food, may affect marine survival of chum.

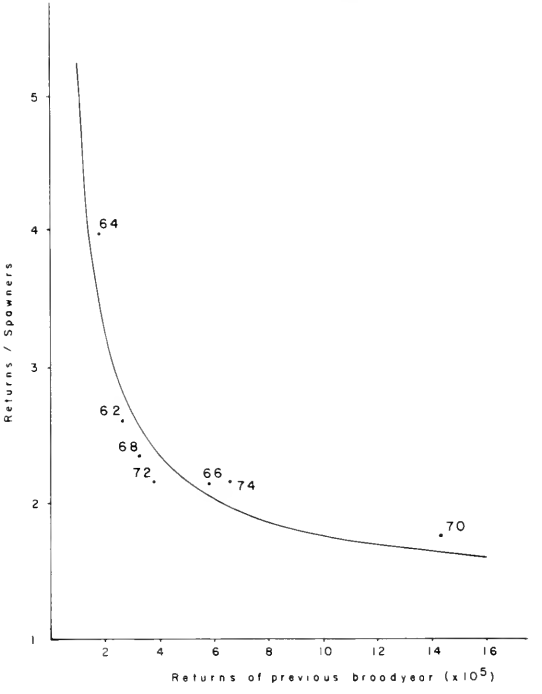

FIGURE 9.—Ratio of returns/spawners for even-numbered brood years of Fraser River chum versus chum abundance in previous brood year.

Pink salmon have been implicated in the present study as impacting population dynamics of Fraser River chum salmon during odd brood

years. Multiple regression was used to describe the effect of pink salmon on chum salmon fry survivals by:

$$\frac{R}{S} = a\,\frac{S}{P} + b(D) + c \qquad (10)$$

where R = total returns from a given brood year
S = spawning escapement of chum salmon that produced a given brood year
P = spawning excapement of pink salmon in same brood year
D = median time of downstream pink salmon fry migration minus median for chum salmon fry in days
c = regression constant.

The analysis yielded:

Variable	*Coefficient*	*SE*	*t*
S/P	13.268	4.928	2.69
D	0.136	0.034	3.93
Constant	−1.469		

The regression was significant ($F = 9.60$, df = 2, and 3, $P<0.05$) and accounted for 85% of the variation in R/S in odd brood years ($R = 0.92$). The chum salmon R/S ratio increases the earlier that chum salmon fry migrate downstream relative to pink salmon fry (Table 6). If chum salmon escapement is 10% of that of pink salmon, then the time of the median downstream migration of chum salmon fry must be at least 9 d earlier than that of pink salmon fry if the chum salmon spawners are just to replace themselves (R/S = 1.0) (Fig. 10). However, if chum salmon escapement is 30% of the pink salmon escapement and chum salmon fry still have a 9-d advantage over pink salmon fry, then the R/S ratio for chum salmon will be between 3.0 and 4.0, as happened for the 1969 brood year (Fig. 10). The chum salmon R/S ratio will still be between 3.0 and 4.0 if the chum salmon escapement is 15% of the pink salmon escapement, provided the chum salmon fry have at least a 19-d advantage over the pink salmon fry, similar to the 1965 brood year (Fig. 10).

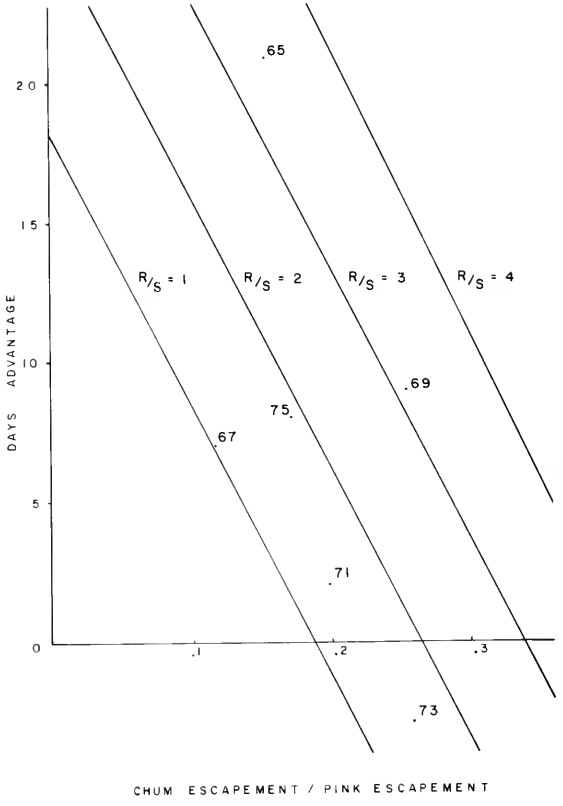

FIGURE 10.—Contour plot for returns/spawners for odd-numbered brood years of Fraser River chum in relation to timing of pink and chum fry migrations and relative spawning escapements of pink and chum. Contour lines of R/S = 1.0, 2.0, 3.0, and 4.0 are plotted.

TABLE 6.—Dates when 50% of the fry were estimated to have migrated downstream and estimated spawning escapements for odd-numbered brood years, 1965-77.

Brood year	Date of 50% fry migration		Spawning escapements ($\times 10^3$)	
	Chum	Pink	Chum	Pink
1965	11 April	2 May	185.0	1,191.1
1967	17 April	24 April	212.0	1,831.4
1969	15 April	24 April	390.0	1,529.5
1971	3 May	5 May	356.7	1,803.8
1973	19 April	16 April	453.0	1,754.1
1975	15 April	23 April	235.3	1,367.3
1977	20 April	25 April	538.8	2,387.8

DISCUSSION

Mean lengths at maturation for 4-yr-old chum salmon in the present study were found to be significantly correlated with oceanic water temperatures in the penultimate growing season but not in the final one. Helle (1979) found that oceanic

environmental factors during the final ocean year strongly influenced length at maturity of chum salmon from Olsen Creek, Alaska. The causes of the different results of the two studies are uncertain, but may in some way be related to the timing of the attainment of a threshold length for spawning.

The fecundity of Fraser River chum salmon (3,250 eggs/female) reported in the present study was greater than that reported by Foerster and Pritchard (1936) for Fraser River chum salmon (2,943 eggs/female), for Nile Creek chum salmon (2,726 eggs/female) (Neave 1953), and for Hooknose Creek chum salmon (2,083-3,097 eggs/female) (Hunter 1959). Only a few of the mean fecundities listed by Bakkala (1970) for North American and Asian chum salmon were greater than that of Fraser River chum salmon. However, size and age compositions of chum salmon sampled for fecundity in the former studies were unavailable, and it may be that larger sized chum salmon were sampled in the Fraser than in other areas because smaller females may have avoided the test fishery.

In chum salmon, males have been reported to predominate in the early part of the run and females in the later part (Gilbert 1922; Henry 1954). In the present study, sex ratios as measured by the test fishery remained relatively constant during the fall upriver migration. This result was probably due to differences in run timing of stocks in the Fraser River, so that stocks in different stages of completeness of the run were sampled at the same time, and thus temporal shifts in sex ratios may have been obscured.

Freshwater and marine survival of Fraser River chum salmon have varied about sixfold and fivefold, respectively. Rainfall and gravel permeability have been implicated in variable freshwater survival elsewhere, with higher rainfall in the fall (except in flood years) and looser, more permeable gravel resulting in higher survival (Wickett 1958). Freshwater survival of chum salmon in Hooknose Creek was inversely related to the total number of pink and chum salmon eggs deposited (Hunter 1959). The present study indicated that freshwater survival of Fraser River chum salmon was inversely related to the amount of winter rainfall, and that much of the variability in freshwater survival was attributable to interactions among temperature, rainfall, and egg abundance.

Mortality among young fry has been suggested to be a major influence in determining the abundance of returning adults from a brood year of pink or chum salmon (Neave 1953; Hunter 1959; Parker 1965). Egg-to-fry survival in Fraser River chum salmon was largely dependent upon physical environmental fluctuations, whereas fry-to-adult survival may be dependent upon chum and pink salmon abundance. The effects of favorable or unfavorable environmental conditions during incubation appear to be compensated for by density-dependent responses of survival during the marine life history stage of chum salmon. Density-dependent survival during the marine residence period has been suggested for several *Oncorhynchus* species, with possible interactions within and among brood years (Peterman 1978). The present study indicated that for even brood years of Fraser River chum salmon, marine survival may be inversely associated with the abundance of the previous brood year, which suggests that the number of returns from a brood year is not determined until the mixing of underyearlings and older chum salmon in the ocean. Although early fry mortality is undoubtedly heavy in chum salmon, as it is in other marine fish, and although it has been suggested that the determination of year-class abundance occurs soon after hatching in marine fishes (Cushing and Harris 1973), some evidence does suggest that year-class abundance is not determined in the first year of life of marine fishes (Ponomarenko 1973; Lett et al. 1975).

The present study indicated that the mean age of returns of a brood year increased with brood year abundance. Similar observations have been reported by Birman (1951) for chum salmon in the Amur River in the Soviet Union and Helle (1979) for chum salmon in Olsen Creek in Alaska. This result implies that growth during ocean residence is density-dependent, as has been reported in other marine fishes (Sonina 1965; Paloheimo and Kohler 1968; Templeman et al. 1978). Competition for food may be one of the mechanisms of this density-dependence. The present study also indicated that higher marine water temperatures were accompanied by increased growth rates, as indicated by annual variability in size of returning 4-yr-old chum salmon.

The present study suggests that there may be competition between chum and pink salmon fry in the Fraser River estuary or Strait of Georgia. Phillips and Barraclough (1978) found that chum salmon fry in the Strait of Georgia near the Fraser estuary were larger in 1967 and 1969 when

pink salmon fry abundance would be low than those in 1966 and 1968 when pink salmon fry would be abundant. When chum and pink salmon fry migrated at similar times, chum salmon fry-to-adult survival was lower than when chum salmon fry migrated earlier than pink salmon fry. Pink salmon grow faster than do chum salmon (Ricker 1964), and this faster growth rate may allow them to outcompete chum salmon fry for food. The influence of pink salmon on egg-to-fry survival of chum salmon was not examined, but we expect it would be minimal relative to environmental influences as pink salmon spawn earlier in the Fraser River than do chum salmon.

The present study suggests some areas that need to be explored further. Interspecific interactions between pink and chum salmon fry may be investigated by marking and varying the size and time of release of chum salmon fry in years when pink salmon fry are present and measuring rates of adult returns for these sets of fry, similar to the studies of Fraser et al. (1978) for chum on the Big Qualicum River and Bilton (1978) for coho salmon, *Oncorhynchus kisutch*.

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TROPHIC PATTERNS AMONG LARVAE OF FIVE SPECIES OF SCULPINS (FAMILY: COTTIDAE) IN A MAINE ESTUARY

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ABSTRACT

The food habits and trophic relationships of larvae of five species of marine cottids—*Myoxocephalus aenaeus*, *M. octodecemspinosus*, *M. scorpius*, *Triglops murrayi*, and *Hemitripterus americanus*—were examined and compared during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Overall feeding incidence was high with <14% of the larvae in any species having empty guts. Larvae of all five species began to feed before yolk absorption was complete.

Among the five species, *M. aenaeus* and *M. octodecemspinosus* were most similar in mouth size, prey size, and dominant prey—adult *Microsetella norvegica* in January and February (winter) and *Balanus* nauplii in March (early spring). Mouth size, prey size, and dominant prey in early spring (*Balanus* nauplii) of *Myoxocephalus scorpius* were similar to the other species of *Myoxocephalus*, but the most frequently ingested prey in winter was the centric diatom, *Coscinodiscus* sp. *Triglops murrayi* larvae had relatively larger mouths and ingested somewhat larger prey than similar-sized *Myoxocephalus* larvae, feeding primarily on adult *Pseudocalanus minutus* in both winter and early spring. Although mouth sizes of *H. americanus* and *T. murrayi* larvae were similar, the diet of *H. americanus* was composed almost exclusively of fish larvae, primarily other cottids.

The high incidence of ingestion of *Balanus* nauplii by *Myoxocephalus* and *T. murrayi* in early spring may indicate some degree of density-dependent food utilization by those larvae. Yet other prey, adult *Temora longicornis* and epibenthic harpacticoid copepods, appeared to be preferred over other presumably more abundant zooplankton.

Percent diet overlap was greatest among the three species of *Myoxocephalus* and, except between *M. aenaeus* and *M. octodecemspinosus*, was lower in winter when mean plankton volume (an approximate measure of food supply) was low. Observed differences in vertical distribution resulting in partial spatial segregation of *M. aenaeus* and *M. octodecemspinosus* larvae may reduce competition for food between the two species, thus allowing the consistently high degree of dietary overlap between them.

Prey size (maximum carapace width) at first feeding ranged from 100 to 375 μm among the three species of *Myoxocephalus* and >800 μm for *H. americanus*. There was no dramatic change in prey types or sizes with increasing larval size. Larvae of the five species of cottids were found to most closely resemble hake (genus *Merluccius*) in prey size relationships.

There have been relatively few detailed descriptions of the food habits of marine fish larvae despite the reputed importance of starvation as a primary cause of mortality in the sea (Hunter 1976). Our generalized concept of early feeding ecology in marine fishes is based mostly on highly fecund species whose larvae hatch from small planktonic eggs at 2-3 mm in length with undeveloped eyes and mouths (Arthur 1976; Last 1978a, b; Sumida and Moser 1980). Little is known of trophic relations among larvae of fishes such as the cottids which deposit relatively few, large, demersal eggs and whose planktonic larvae hatch at sizes ≧5 mm, in a relatively advanced stage of development with pigmented eyes and functional mouths (Laroche 1980). Fishes with widely divergent ontogenies would be expected to also have different early trophic relations, whose comparisons may yield further insights into processes controlling survival in the sea.

The kinds of food used in most laboratory studies of foraging behavior, feeding efficiencies, and growth of fish larvae are usually organisms which are easily cultured in quantity but are not natural larval fish prey, or which are known size fractions of wild plankton whose species composition is only approximately known. Laboratory results, based solely on unnatural and/or single prey, or prey described by size only, may have little relevance to the real situation in the sea. It is not unreasonable to suspect that different kinds (and sizes) of prey may sig-

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nificantly affect the feeding and growth of fish larvae. For these reasons, there is a need for additional detailed descriptions of natural prey so that laboratory studies can be designed to investigate the effects of these prey organisms on larval fish behavior, metabolism, and growth.

This study was undertaken to examine and compare the food habits and trophic relationships of the larvae of five species of marine cottids—*Myoxocephalus aenaeus*, *M. octodecemspinosus*, *M. scorpius*, *Triglops murrayi*, and *Hemitripterus americanus*—during winter and early spring when they cooccur at peak abundance in the Damariscotta River estuary, Maine. Data are presented on feeding incidence, diet composition, diet overlap, larval mouth size, and prey size. Trophic patterns are examined with respect to possible interspecific competition and the influence of relative prey abundance and morphology on foraging. Aspects of the feeding ecology of these larvae are compared with the early feeding ecology of other marine fishes.

MATERIALS AND METHODS

Larvae used in diet analyses were collected in surface and bottom tows of a 1 m, 360 μm mesh conical plankton net which was mounted atop a 1.3 m wide × 45.7 cm high Blake trawl (a type of beam trawl). Although larvae were collected throughout the Damariscotta River, a drowned river valley opening into the Gulf of Maine and located on the central Maine coast, most specimens were captured in the middle basin of the estuary (Laroche 1980). *Myoxocephalus* (*M. aenaeus*, *M. octodecemspinosus*, and *M. scorpius*) and *T. murrayi* larvae were collected, for the most part, on these dates in 1973: 22 January; 6, 20, 21 February; and 5, 6, 19, 20 March. From 26 to 30% of larvae of the four species used in diet analyses were taken in surface tows and 70 to 74% were taken in bottom tows. Larvae of *H. americanus* were rare in collections; therefore, all specimens collected during the period January-April 1972-74 were used in diet analyses.

Prior to preservation in 10% Formalin[2] in the field, an unquantified amount of MS-222 (tricaine methanesulfonate) was added to each sample. The sample was gently swirled as the anesthetic dissolved larvae became inactive. This procedure eliminated defecation and/or regurgitation subsequent to capture.

Before removal of the gut, standard length (SL, to nearest 0.1 mm) and upper jaw length (i.e., distance from symphysis to posterior margin of maxillary along the ventral aspect, to nearest 0.01 mm) were measured using an ocular micrometer in a stereomicroscope. Jaw length rather than gape was used as a measure of potential size of the mouth opening because jaw length was not affected by whether the mouth was opened or closed at the time of preservation and could, therefore, be measured more consistently and precisely. Larvae were placed in a cavity of a double-depression glass slide, and the entire gastrointestinal tract from esophageal sphincter to anus was gently pulled intact from the abdominal cavity. At this time the presence or absence of yolk was noted, and an estimate was made of the quantity of yolk present: one-fourth, one-half, three-fourths of abdominal cavity full or only a remnant remaining. The gut was placed in the other, water-filled cavity of the slide, and the gastric and pyloric regions were teased apart separately using two fine probes. The presence or absence of food items in each of these regions was noted.

Food items were identified to the lowest taxon possible and counted except for undigestable prey remains, such as setae, and unrecognizable debris. *Pseudocalanus* eggs, which were probably ingested with the brooding females, and small diatoms (in March samples only) were likewise not counted. Maximum body width or diameter of most food items was measured.

Larvae were grouped into arbitrarily chosen size intervals, based on overall size distributions, to facilitate intra- and interspecific diet comparisons. Percent frequency of occurrence (%*FO*) and percent of total number (%*N*) of prey ingested by larvae in each size group were calculated for each food category. An estimate of the relative importance of each food category was obtained by multiplying %*FO* by %*N*. Diet overlap was measured using the Schoener index (1970):

$$\alpha = 100\ [1 - 0.5 \sum_{i=1}^{n} /p_{xi} - p_{yi}/],$$

where p_{xi} = proportion (percent by number) of food category i in the diet of species x; p_{yi} = proportion (percent by number) of food category i in the diet of species y; and n = the number of food

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

categories. Percent by volume or weight is, in most cases, more useful than $\%N$ or $\%FO$ in measuring diet overlap. However, for predators like larval *Myoxocephalus* and *T. murrayi* whose prey are similar in size (Fig. 1), calculation of the Schoener index using $\%N$ and $\%FO$ produces a relatively unbiased estimate of diet overlap (Wallace 1981).

Settled volumes of the ichthyoplankton samples were measured by displacement method in either a 100 or 250 ml graduated cylinder after large jellyfish and macrophytic algae or other large plant debris were removed.

RESULTS

Feeding Incidence

The percentage of cottid larvae with empty guts ranged from 0 to 13 depending on the species, with *T. murrayi* having the lowest overall incidence of empty guts and *H. americanus* the highest (Table 1). Only *M. aenaeus* and *M. scorpius* had equal or higher percentages of empty guts in January and February than in March. In addition to this high incidence of feeding, many larvae examined had begun to feed before yolk absorption was complete (Table 1). A remnant of yolk (often sizeable) was found attached to or closely associated with the liver in feeding larvae over a wide size range: 5.3-9.5 mm SL in *M. aenaeus*; 7.2-11.5 mm SL in *M. octodecemspinosus*; 7.5-10.4 mm SL in *M. scorpius*; 8.5-12.0 mm SL in *T. murrayi*; and 12.0-15.9 mm SL in *H. americanus*.

Among the three species of *Myoxocephalus* larvae with three-fourths of the abdominal cavity filled with yolk ($N = 33$), about 80% had food in their guts. The number of food items found in these larvae ranged from 1 to 4 in *M. aenaeus*, 2 to 12 in *M. octodecemspinosus*, and 1 to 21 in *M. scorpius*. No yolk-sac larvae of *T. murrayi* were collected. Of the seven *H. americanus* larvae with prominent yolk sacs, only two had empty guts. Each of the other larvae contained one food item.

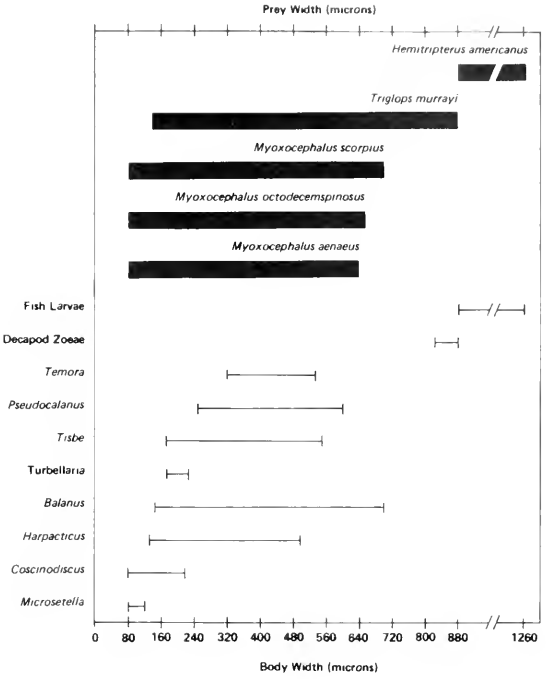

FIGURE 1.—Range in maximum body width (microns) of the major prey ingested by larvae of five species of cottids in the Damariscotta River estuary, Maine.

Diet Composition

Gut contents were examined of 147 *M. aenaeus*, 5.3-9.5 mm SL; 106 *M. octodecemspinosus*, 7.2-12.4 mm SL; 87 *M. scorpius*, 7.5-13.4 mm SL; 58 *T. murrayi*, 8.5-18.1 mm SL; and 24 *H. americanus*, 12.0-16.2 mm SL (Tables 2-10). Percent number of *Coscinodiscus* sp. was calculated only

TABLE 1.—Incidence of *Myoxocephalus*, *Triglops*, and *Hemitripterus* larvae with empty guts, and those with both food and a remnant of yolk present. (N = number of larvae examined.)

	January-February			March		
Species	N	% empty	% with yolk + food	N	% empty	% with yolk + food
Myoxocephalus aenaeus	18	6	94	129	6	75
M. octodecemspinosus	31	0	100	75	5	66
M. scorpius	18	11	89	69	0	91
Triglops murrayi	22	0	73	36	3	6
	January-April					
Hemitripterus americanus	24	13	83			

TABLE 2.—Summary of food habits of 18 *Myoxocephalus aenaeus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	5.3-6.4				6.5-7.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	7.1	1	0.8
Calanoid copepods:								
Temora longicornis					1	7.1	3	2.5
Harpacticoid copepods:								
Microsetella norvegica	3	75.0	9	81.8	14	100.0	104	85.2
Tisbe spp.					2	14.3	2	1.6
Unidentified								
Adults and copepodites					1	7.1	1	0.8
Coscinodiscus sp	1	25.0	2	18.2	7	50.0	11	9.0
Total no. food items			11				122	
Number larvae examined	4				14			
Number larvae empty	1				0			

TABLE 3.—Summary of the food habits of 129 *Myoxocephalus aenaeus* larvae captured on 5, 6, 19, and 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)															
	5.5-6.4				6.5-7.4				7.5-8.4				8.5-9.5			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	12	100.0	34	61.8	43	93.5	158	57.5	37	88.1	115	42.6	20	95.2	90	54.9
Calanoid copepods:																
Temora longicornis					3	6.5	4	1.5	9	21.4	16	5.9	4	19.0	5	3.0
Harpacticoid copepods:																
Microsetella norvegica	4	33.3	9	16.4	24	52.2	47	17.1	23	54.8	51	18.9	13	61.9	12	7.3
Tisbe spp.					10	21.7	13	4.7	10	23.8	20	7.4	5	23.8	9	5.5
Harpacticus spp.					2	4.3	2	0.7	13	31.0	17	6.3	6	28.6	9	5.5
Zaus sp.					2	4.3	2	0.7	3	7.1	4	1.5				
Unidentified.																
Adults and copepodites					5	10.9	6	2.2	3	7.1	4	1.5	1	4.8	2	1.2
Unidentified copepod nauplii					1	2.2	1	0.4					1	4.8	25	15.2
Turbellaria	3	25.0	4	7.3	13	28.3	19	6.9	12	28.6	23	8.5	4	19.0	7	4.3
Ostracoda					2	4.3	2	0.7								
Unidentified invertebrate eggs:																
Single	1	8.3	7	12.7	7	15.2	21	7.6	2	4.8	13	4.8				
Sacs	1	8.3	1	1.8					6	14.3	7	2.6	4	19.0	5	3.0
Coscinodiscus sp.	3	25.0	—		10	21.7	—		10	23.8	—		7	33.3	—	
Setae	2	16.7	—		5	10.9	—		11	26.2	—		3	14.3	—	
Unrecognizable debris	5	41.7	—		13	28.3	—		20	47.6	—		12	57.1	—	
Total no. food items			55				275				270				164	
Number larvae examined	17				49				42				21			
Number larvae empty	5				3				0				0			

in January-February and not in March when barnacle nauplii were the principal prey of larvae, because it is likely that some proportion of these diatom cells were released from the guts of *Balanus* nauplii during digestion. Cells ≤25 μm in diameter were found inside undigested *Balanus* nauplii taken from the guts of cottid larvae. Flatworms (Turbellaria) ingest diatoms whole (Jennings 1957) and these may also have contributed *Coscinodiscus* cells. Most of the calanoid and harpacticoid copepods ingested by cottid larvae were adults and, for *Temora longicornis*, mostly females. Bundles of setae of undetermined origin seemed to accumulate in the guts of cottid larvae. The most likely sources of these are the appendages of *Microsetella* and *Balanus* nauplii.

Diet Comparisons

Relative importance of each prey taxon was estimated from the product of %*FO* and %*N*. Major prey (%*FO* × %*N*>100) of only similar-sized larvae were ranked according to this value and compared for seasonal as well as inter- and intraspecific differences (Tables 11, 12). In general, the same trophic patterns were present among larvae in size groups not included in these comparisons (Tables 2-10).

In January and February the dominant prey of

TABLE 4.—Summary of the food habits of 31 *Myoxocephalus octodecemspinosus* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)							
	7.2-8.4				8.5-9.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					2	28.6	2	1.7
Calanoid copepods:								
Temora longicornis	7	29.2	8	2.5	7	100.0	28	23.3
Harpacticoid copepods:								
Microsetella norvegica	24	100.0	284	89.3	7	100.0	65	54.2
Tisbe spp.	2	8.3	2	0.6				
Harpacticus spp.	2	8.3	2	0.6				
Unidentified								
Adults and copepodites	3	12.5	3	0.9	2	28.6	3	2.5
Unidentified copepod nauplii	2	8.3	3	0.9	1	14.3	2	1.7
Ostracoda	1	4.2	1	0.3				
Unidentified invertebrate eggs								
Single					2	28.6	20	16.7
Coscinodiscus sp.	3	12.5	15	4.7				
Setae	1	4.2	—					
Total no. food items			318				120	
Number larvae examined	24				7			
Number larvae empty	0				0			

both *M. aenaeus* and *M. octodecemspinosus* was *Microsetella norvegica*, while *Coscinodiscus* sp. dominated the diet of *Myoxocephalus scorpius* larvae. *Coscinodiscus* sp. cells are bright green in color and the digestive tracts of *M. scorpius* larvae observed in the field before preservation appeared to be this same color. Unlike similar-sized *M. octodecemspinosus* and *M. scorpius*, *Triglops murrayi* larvae fed primarily on adult *Pseudocalanus minutus* and calanoid copepodites, which were largely digested but most resembled, and probably were, immature *Pseudocalanus*. There appeared to be no distinct change in dominant prey types as larvae grew within the size ranges examined. The largest *M. octodecemspinosus* and *M. scorpius* larvae ingested more kinds of prey than smaller larvae, but the reverse was true for *T. murrayi*.

In March, the overwhelmingly dominant prey of all three species of *Myoxocephalus* were *Balanus* nauplii. *Microsetella* ranked second in importance among 7.5-9.5 (9.4) mm SL *Myoxocephalus aenaeus* and *M. octodecemspinosus* larvae, but was replaced by adult *Temora longicornis* in 9.5-12.4 mm SL *M. octodecemspinosus*. No other prey of *M. scorpius* larvae at any size approached the importance of *Balanus* nauplii which were nearly the exclusive prey of this species in March. Mean number of nauplii per *M. scorpius* larva ranged from 12 to 16 depending on larval size, whereas the range in mean number for the other two species of *Myoxocephalus* was only 3-8 nauplii/larva. As in January and February, *Pseudocalanus* dominated the diet of *T. murrayi* larvae in four of six size groups. *Balanus* nauplii ranked second in importance in four size groups, and ranked first in the largest size group. Other fish larvae, primarily *M. aenaeus*, were nearly the exclusive prey of all *H. americanus* larvae examined. Up to four prey larvae were found in the gut of a single *H. americanus* larva, and a 13 mm SL rockgunnel, *Pholis gunnellus*, larva was found coiled up inside the gut of a 13 mm SL specimen. There was no dramatic change in prey types ingested among the five species with increasing larval size. Only the change in the second-ranked prey of *M. octodecemspinosus* larvae from *Microsetella* to *Temora* may have been related to increased size.

The most important seasonal change in diet among cottid larvae was replacement of *Coscinodiscus* sp. and, to a lesser extent, *Microsetella* by *Balanus* nauplii. Barnacle nauplii also became a relatively important component of the diet of *T. murrayi* larvae in March but *Pseudocalanus* continued to dominate the diet of larvae in most size groups.

Diet Overlap

Diet overlap was measured among larvae of four species of cottids (*H. americanus* excluded because of its obviously unique diet), using the Schoener index (1970) which describes the relative amount of dietary overlap between species pairs on a scale of 0 = no overlap to 100 = com-

TABLE 5.—Summary of the food habits of 75 *Myoxocephalus octodecemspinosus* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	7.5-8.4				8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	4	80 0	17	39 5	23	95.8	117	45.3	21	87 5	126	61.8	11	84 6	76	76.8	3	60.0	42	77.8
Calanoid copepods																				
Temora longicornis	1	20.0	2	4 7	8	33.3	14	5.4	13	54.2	36	17.6	9	69.2	17	17.2	4	80.0	11	20.4
Harpacticoid copepods																				
Microsetella norvegica	3	60.0	19	44 2	16	66.7	51	19.8	11	45.8	26	12.7	1	7.7	2	2.0				
Tisbe spp.					3	12.5	3	1.2	2	8.3	3	1.5	1	7.7	1	1.0				
Harpacticus spp	1	20.0	2	4 7									1	7.7	1	1.0				
Unidentified																				
Adults and copepodites	1	20 0	1	2.3	1	4 2	1	0.4	2	8.3	2	1.0	1	7.7	1	1.0				
Unidentified invertebrate eggs																				
Single	1	20.0	1	2.3	6	25.0	69	26.7	1	4.2	9	4.4	1	7.7	1	1.0	1	20.0	1	1.9
Sacs	1	20.0	1	2 3	3	12.5	3	1.2	1	4.2	2	1.0								
Coscinodiscus sp.	2	40.0	—		2	8.3	—		3	12.5	—		2	1.5			2	40.0	—	
Setae	2	40 0	—		5	20.8	—		6	25.0	—		3	2.3	—					
Unrecognizable debris	2	40 0	—		7	29 2	—		9	37.5	—		7	5 4	—		2	40.0	—	
Total no. food items			43				258				204				99				54	
Number larvae examined	7				25				25				13				5			
Number larvae empty	2				1				1				0				0			

TABLE 6.—Summary of the food habits of 18 *Myoxocephalus scorpius* larvae captured on 22 January and 6 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)											
	7.5-8 4				8.5-9.4				9 5-10.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	11.1	2	0.9	3	100 0	3	3.1
Calanoid copepods:												
Temora longicornis					1	11.1	1	0.5	2	66.7	3	3.1
Pseudocalanus minutus					1	11.1	1	0.5				
Unidentified									1	33.3	1	1.0
Harpacticoid copepods:												
Microsetella norvegica	2	50.0	2	6.1	3	33.3	7	3 2	1	33.3	2	2.0
Tisbe spp.									1	33.3	1	1.0
Harpacticus spp.					2	22.2	2	0.9	1	33.3	1	1.0
Zaus sp.					2	22.2	3	2.8				
Unidentified:												
Adults and copepodites					3	33.3	3	1.4	3	100.0	10	10.2
Nauplii					1	11.1	27	12.5	1	33.3	30	30.6
Unidentified invertebrate eggs:												
Single					3	33.3	62	28.7	1	33.3	25	25.5
Coscinodiscus sp.	3	75.0	31	93 9	8	88.9	108	50.0	3	100.0	22	22.4
Unrecognizable debris	1	25.0	—		2	22 2	—		1	33.3	—	
Total no. food items			33				216				98	
Number larvae examined	6				9				3			
Number larvae empty	2				0				0			

TABLE 7.—Summary of food habits of 69 *Myoxocephalus scorpius* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	8.5-9.4				9.5-10.4				10.5-11.4				11.5-12.4				12.5-13.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii	14	100.0	165	94.3	28	96.6	426	77.3	12	100.0	182	90.1	8	100.0	120	91.6	6	100.0	95	93.1
Calanoid copepods:																				
Temora longicornis					8	27.6	12	2.2	2	16.7	8	4.0	2	25.0	4	3.1	1	16.7	1	1.0
Unidentified:																				
Adults and copepodites					5	17.2	5	0.9	1	8.3	2	1.0	2	25.0	2	1.5				
Harpacticoid copepods:																				
Tisbe spp.					9	31.0	11	2.0	3	25.0	3	1.5	2	25.0	2	1.5	3	50.0	3	2.9
Harpacticus spp.					7	24.1	9	1.6	3	25.0	3	1.5	1	12.5	1	0.8				
Zaus sp.	1	7.1	1	0.6	3	10.3	3	5.4					1	12.5	2	1.5	1	16.7	1	1.0
Unidentified																				
Adults and copepodites	1	7.1	1	0.6	2	6.9	8	1.5	1	8.3	2	1.0					1	16.7	1	1.0
Unidentified invertebrate eggs:																				
Single	2	14.3	8	4.6	5	17.2	77	14.0	2	16.7	2	1.0								
Sacs																	1	16.7	1	1.0
Coscinodiscus sp.	2	14.3	—		5	17.2	—		3	25.0	—		3	37.5	—		1	16.7	—	
Setae					3	10.3	—		1	8.3	—		2	25.0	—		1	16.7	—	
Unrecognizable debris	5	35.7	—		10	34.5	—		5	41.7	—		4	50.0	—		2	33.3	—	
Total no. food items			175				551				202				131				102	
Number larvae examined	14				29				12				8				6			
Number larvae empty	0				0				0				0				0			

TABLE 8.—Summary of the food habits of 22 *Triglops murrayi* larvae captured on 22 January and 6, 20, 21 February 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																			
	8.5-8.9				9.0-10.4				10.5-11.4				11.5-12.4				12.5-14.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Balanus nauplii																				
Calanoid copepods:																	1	33.3	1	2.2
Temora longicornis	1	20.0	2	10.0	1	20.0	1	2.9					2	50.0	8	18.6	2	66.7	7	15.6
Pseudocalanus minutus	5	100.0	9	45.0	5	100.0	20	57.1	5	100.0	17	77.3	4	100.0	31	72.1	3	100.0	24	53.3
Unidentified:																				
Adults					1	20.0	1	2.9					1	25.0	1	2.3				
Copepodites	4	80.0	8	40.0	5	100.0	13	37.0	3	40.0	5	22.7	3	75.0	3	7.0	2	66.7	12	26.7
Nauplii																	1	33.3	1	2.2
Pseudocalanus eggs					1	20.0	—		3	40.0	—		1	25.0	—					
Harpacticoid copepods:																				
Tisbe sp.	1	20.0	1	5.0																
Unrecognizable debris					2	40.0	—													
Total no. food items			20				35				22				43				45	
Number larvae examined	5				5				5				4				3			
Number larvae empty	0				0				0				0				0			

TABLE 9.—Summary of the food habits of 36 *Triglops murrayi* larvae captured on 5, 6, 19, 20 March 1973. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)																							
	9.0-10.4				10.5-11.4				11.5-12.4				12.5-13.4				13.5-14.4				14.5-15.4				15.5-18.1			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%N	*FO*	%*FO*	*N*	%*N*
Balanus nauplii					1	33.3	7	43.8	2	40.0	21	33.3	2	50.0	15	45.5	4	66.7	33	42.9	5	100.0	31	62.0	9	100.0	59	64.8
Calanoid copepods:																												
Temora longicornis																	2	33.3	2	2.6	3	60.0	8	16.0	2	10.3	9	9.9
Pseudocalanus minutus	2	100.0	6	85.7	2	66.7	7	43.8	3	60.0	6	9.5	4	100.0	16	48.5	6	100.0	29	37.7	3	60.0	8	16.0	7	77.8	14	15.4
Unidentified:																												
Adults					1	33.3	1	6.3	1	20.0	1	1.6													1	11.1	4	4.4
Copepodites	1	50.0	1	14.3					1	20.0	1	1.6	2	50.0	2	6.1	2	33.3	2	2.6	1	20.0	1	2.0	1	11.1	1	1.1
Pseudocalanus eggs					2	66.7	—						1	25.0	—		2	33.3	—		1	20.0	—		3	33.3	—	
Unidentified																												
Harpacticoid copepods									1	20.0	1	1.6																
Cyclopoid copepods					1	33.3	1	6.3																				
Decapod zoea																	1	16.7	1	1.3	1	20.0	1	2.0	4	44.4	4	4.4
Unidentified invertebrate eggs									2	40.0	33	52.4					1	16.7	10	13.0	1	20.0	1	2.0				
Unrecognizable debris									1	20.0	—						2	33.3	—		3	60.0	—		8	88.9	—	
Total no. food items			7				16				63				33				77				50				91	
Number larvae examined	4				3				5				4				6				5				9			
Number larvae empty	1				0				0				0				0				0				0			

TABLE 10.—Summary of the food habits of 24 *Hemitripterus americanus* larvae captured on 22 January 1974; 16 February 1972; 7 March 1972; 5, 6, 20 March 1973; 6 March 1974; and 12 April 1972. %*FO* = percent frequency of occurrence (*FO*) among larvae containing food; %*N* = percent of the total number (*N*) of food items ingested by larvae in that size group.

	Size range (mm)															
	12.0-13.4				13.5-14.4				14.5-15.4				15.5-16.4			
Food item	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*	*FO*	%*FO*	*N*	%*N*
Decapod zoea					1	20.0	1	20.0								
Fish larvae[1]	8	100.0	9	100.0	4	80.0	4	80.0	4	100.0	6	100.0	4	100.0	8	100.0
Total no. food items			9				5				6				8	
Number larvae examined	10				6				4				4			
Number larvae empty	2				1				0				0			

[1]Includes:
1 - *Pholis gunnellus* (~13 mm SL)
1 - *Lumpenus lampretaeformis*
12 - *Myoxocephalus aenaeus* (~5-6 mm SL)
1 - *M. octodecemspinosus* (~7-8 mm SL)
1 - *Triglops murrayi*
6 - Unidentified cottid larvae
5 - Unidentified fish larvae.

TABLE 11.—Comparison of the major prey of similar-sized cottid larvae from January and February 1973. Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; Cosc = *Coscinodiscus* sp.; $E_{(si)}$ = Invertebrate eggs (single); Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; UCalc = Unidentified calanoid copepodites; UHa or n = Unidentified harpacticoid adults or nauplii.

Myoxocephalus aenaeus			
Size range (mm)	6.5-7.4		
Ranked food items	Mn (8,500) Cosc (450)		
Myoxocephalus octodecemspinosus			
Size range (mm)	7.2-8.4	8.5-9.4	
Ranked food items	Mn (8,900)	Mn (5,420) Tem (2,330) $E_{(si)}$ (478)	
Myoxocephalus scorpius			
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4
Ranked food items	Cosc (7,043) Mn (305)	Cosc (4,445) $E_{(si)}$ (956) UHn (139) Mn (106)	Cosc (2,240) UHn (1,029) UHa (1,000) $E_{(si)}$ (849) BN (300) Tem (200)
Triglops murrayi			
Size range (mm)		8.5-8.9	9.0-10.4
Ranked food items		Ps (4,500) UCalc (3,200) Tem (200) Ts (100)	Ps (5,700) UCalc (3,700)

plete overlap (Fig. 2). Except for the consistently high degree of overlap between the diets of *Myoxocephalus aenaeus* and *M. octodecemspinosus*, overlap among cottid larvae in general

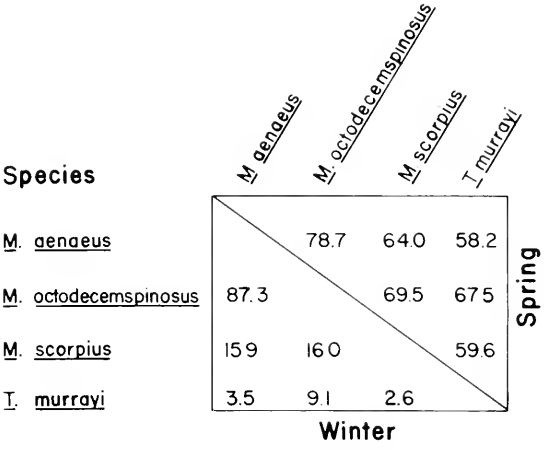

FIGURE 2.—Matrix of Schoener (1970) index values measuring percent diet overlap among species pairs of cottid larvae from winter (January-February) and early spring (March) collections in the Damariscotta River estuary, Maine.

TABLE 12.—Comparison of the major prey of similar-sized cottid larvae from March 1973 (*Myoxocephalus* spp. and *T. murrayi*) and January-April 1972-74 (*H. americanus*). Food items are listed in order of decreasing rank by the value (in parentheses) of the product, % frequency of occurrence × % of total number; only items with a value >100 are presented. Food item abbreviations are: BN = *Balanus* nauplii; DZ = decapod zoea; $E_{(si)}$ = Invertebrate eggs (single); FL = fish larvae; H = *Harpacticus* spp.; Mn = *Microsetella norvegica*; Ps = *Pseudocalanus minutus*; Tem = *Temora longicornis*; Ts = *Tisbe* spp.; Tur = Turbellaria; UCala or c = Unidentified calanoid adults or copepodites; UCyc = Unidentified cyclopoids. (* = tied rank.)

Myoxocephalus aenaeus								
Size range (mm)	7.5-8.4	8.5-9.5						
Ranked food items	BN (3,753) Mn (1,036) Tur (243) H (195) Ts (176) Tem (126)	BN (5,226) Mn (452) H (157) Ts (131)						
Myoxocephalus octodecemspinosus								
Size range (mm)	7.5-8.4	8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4			
Ranked food items	BN (3,160) Mn (2,652)	BN (4,340) Mn (1,321) $E_{(si)}$ (668) Tem (180)	BN (5,408) Tem (954) Mn (582)	BN (6,497) Tem (1,190)	BN (4,668) Tem (1,632)			
Myoxocephalus scorpius								
Size range (mm)		8.5-9.4	9.5-10.4	10.5-11.4	11.5-12.4	12.5-13.4		
Ranked food items		BN (9,430)	BN (7,467) $E_{(si)}$ (241)	BN (9,000)	BN (9,160)	BN (9,310) Ts (145)		
Triglops murrayi								
Size range (mm)			9.0-10.4	10.5-11.4	11.5-12.4	12.5-13.4	13.5-14.4	14.5-15.4
Ranked food items			Ps (8,570) UCalc (715)	Ps (2,921) BN (1,459) *UCala (210) *UCyc (210)	$E_{(si)}$ (2,096) BN (1,459) Ps (570)	Ps (4,850) BN (1,332) UCalc (305)	Ps (3,770) BN (2,275) $E_{(si)}$ (217)	BN (6,200) *Ps (960) *Tem (960)
Hemitripterus americanus								
Size range (mm)						12.0-13.4	13.5-14.4	14.5-15.4
Ranked food items						FL (10,000)	FL (6,400) DZ (400)	FL (10,000)

was greater in early spring (March) than in winter (January and February). Diets of the three species of *Myoxocephalus* usually overlapped more with each other than did any with the diet of *T. murrayi*. This difference was more pronounced in winter than in early spring.

Larval Mouth Size and Prey Width

Because mouth size or gape determines maximum size of prey ingested, the ratio of upper jaw length (mm) to standard length (mm) was used to compare relative mouth sizes among cottid larvae (Blaxter and Hempel 1963; Shirota 1970). Jaw length to standard length ratios were most similar at all stages of development among the three species of *Myoxocephalus* (Table 13). Larvae of *T. murrayi* and *H. americanus*, regardless of stage of development, had larger mouths than *Myoxocephalus* larvae. Only *H. americanus* larvae had jaw teeth within the size range observed.

All food items found in cottid larvae had been swallowed whole. Since fish larvae have been observed to swallow their prey head-first with appendages and setae folded back, the critical dimension of a potential food item is maximum body width (Blaxter 1965; Arthur 1976). Maximum widths of the major prey of larval cottids ranged from 80 to 1,260 μm (Fig. 1). Among individual prey items, *Balanus* nauplii exhibited the widest size range and *Microsetella* the narrowest. The harpacticoid and calanoid copepods were somewhat similar in size, while the largest prey overall were decapod zoea and fish larvae.

Prey size at first feeding was estimated for larvae of *Myoxocephalus* and *H. americanus* from the width of prey found in guts of larvae with three-fourths or more of their abdomens full of yolk. No yolk-bearing larvae of *T. murrayi* were found with this condition. *Myoxocephalus aenaeus* ($N = 14$) ingested *Microsetella* and stage 2 or 3 *Balanus* nauplii ranging in size from 100 to 360 μm. *Myoxocephalus octodecemspinosus* ($N = 5$) ingested only 100 μm wide *Microsetella*. *Myoxocephalus scorpius* ($N = 9$) ingested primarily *Coscinodiscus* and *Microsetella* which ranged from 80 to 220 μm; however, a single *Balanus* nauplius and unidentified harpacticoid copepod were found measuring 375 and 260 μm, respectively. First-feeding *H. americanus* larvae were also primarily piscivorous. Maximum width of most prey larvae (dorsally across the eyes) could not be measured because of advanced state of digestion, but one intact larva measured 950 μm. The only other prey found in yolk-sac *H. americanus* larvae was an 880 μm wide decapod zoea.

No consistent pattern of increased prey size with increased larval size or advanced stage of development was apparent over the size range of cottid larvae observed in these analyses. Overall size range of prey ingested by *Myoxocephalus* and *T. murrayi* larvae overlapped extensively (Fig. 1). Among *Myoxocephalus* larvae, *M. scorpius* ingested slightly larger prey than did the other two species which reflects the greater frequency of *Balanus* nauplii and low incidence of *Microsetella* in its diet. *Triglops murrayi* larvae ate food items over the widest size range and *H. americanus* over the narrowest size range.

DISCUSSION

The incidence of yolk retention in feeding cottid larvae was high over a wide size range, presumably representing a long period of time. Initiation of feeding before complete yolk absorption has been previously observed among larval flatfishes, gadoids, and herring (Blaxter 1965; Last 1978a, b; Sumida and Moser 1980). Arthur (1976), however, never found both yolk and ingested food in larvae of northern anchovy, *Engraulis mordax*; Pacific sardine, *Sardinops sagax*; or jack mackerel, *Trachurus symmetricus*. Food ingestion prior to complete yolk absorption may be advantageous to fish larvae by allowing time for trial-and-error learning, which has been

TABLE 13.—Comparison of relative mouth size among larval cottids using the ratio of upper jaw length (mm) to standard length (SL). N = number of larvae measured.

	Larvae used in diet analysis				Smallest larvae with yolk sac			
			Upper jaw length/SL				Upper jaw length/SL	
Species	N	Mean SL (mm)	Mean	Range	N	Mean SL (mm)	Mean	Range
Myoxocephalus aenaeus	84	7.4	0.11	0.10-0.13	12	6.3	0.10	0.09-0.10
M. octodecemspinosus	72	9.7	0.11	0.09-0.13	15	7.7	0.10	0.09-0.11
M. scorpius	61	10.3	0.12	0.09-0.13	10	8.4	0.11	0.09-0.12
Triglops murrayi	35	13.8	0.13	0.12-0.15	1	7.1	(0.13)	—
Hemitripterus americanus	20	13.9	0.15	0.13-0.17	1	13.0	(0.15)	—

shown to increase feeding success in early larvae (Blaxter 1965; Hunter 1980), as well as by prolonging the time before larvae become totally dependent on an exogenous food supply which is limited in abundance and distribution (Laurence and Rogers 1976). Potential or actual energy deficits prior to or coincident with the initiation of feeding were found to occur in the tautog, *Tautoga onitis* (Laurence 1973), and Pacific sardine, *Sardinops sagax* (Lasker 1962), both relatively fecund species having planktonic eggs and larvae. Yet, deficits based on the amount of yolk absorbed did not occur until after feeding had begun in rainbow trout, *Salmo gairdneri*; brown trout, *Salmo trutta*; bluegill, *Lepomis macrochirus*; and largemouth bass, *Micropterus salmoides*, all of which have relatively low fecundity, and demersal eggs and larvae (Laurence 1973). Although energy budgets have not been described for them, it is likely that cottids have yolk-utilization characteristics similar to this latter group of fishes.

The relatively higher incidence of empty guts among the almost exclusively piscivorous larvae of *H. americanus* may also be related to trophic energetics. Since fish larvae probably supply more energy per unit effort as prey than do crustaceans because of larger size and lack of indigestible exoskeletons, ingestion of single, large, highly digestible prey would reduce the need for continuous foraging. Larvae of *H. villosus* in the Japan Sea, like those of its congener in the Gulf of Maine, also feed on other fish larvae (Okiyama and Sando 1976). Most reports of piscivorous larvae have come from observations of laboratory-reared larvae, particularly scombroid fishes (Beyer 1980; Hunter 1980).

The larval diets of four of five species of cottids in the Damariscotta River estuary were distinctly different, despite similarities in mouth size and morphology and the absence of obvious specialized morphological adaptations for feeding. Last (1978a) also observed differences in larval diets among pleuronectiform fishes in the North Sea and concluded that this represented a mechanism whereby direct competition for food is avoided. There are many theoretical and practical difficulties in assessing the significance of competition as a cause of dietary divergence in fishes (Zaret and Rand 1971; Weatherly 1972), yet existence of competition among tropical stream fishes has been inferred from observed reductions in diet overlap during periods of lowered food supply (Zaret and Rand 1971). Comparisons of dietary overlap and food supply among the larvae of *Myoxocephalus* and *Triglops* species during winter and early spring indicated a similar pattern. The lowest values of percent diet overlap, i.e., occurrence of the most dissimilar diets, among five of six possible pairs of species combinations occurred in January and February, and coincided with lowest prey abundance as indicated by the lower mean plankton volume (an approximate measure of food supply) of the two periods compared, 16.8 ml ($n = 22$) vs. 31.0 ml ($n = 25$) in March.

Percentage diet overlap between *M. aenaeus* and *M. octodecemspinosus*, whose larvae were the most abundant in the estuary (Laroche 1980) and who had the most similar food habits, remained relatively high and constant through winter and early spring. Some mechanism other than dietary shifts, i.e., changes in dominant prey, may act to reduce competition between larvae of these two species. Although both species were more abundant 1.5 m above the bottom than in the upper 1.5 m during winter and spring months, *M. aenaeus* larvae were 5 times more abundant while *M. octodecemspinosus* were only 1.7 times more abundant (Laroche 1980). Such relative differences in vertical distribution resulted in spatial separation of most *M. aenaeus* and *M. octodecemspinosus* larvae. If competition is indeed an important factor in diet determination among cottid larvae, this spatial separation may explain the high degree of dietary overlap between these two species.

Density-independent food exploitation (Hyatt 1979) by fish larvae has not been demonstrated by quantitative comparisons of prey abundance in larval guts to their abundance in the plankton. Blaxter (1965) cited numerous examples, mostly qualitative, of apparent selection among herring larvae for specific taxa of copepod and diatom prey over other prey which were more abundant in the plankton. Qualitative comparisons of the composition and relative abundance of the zooplankton present during winter and spring months of 1972 in the Damariscotta River estuary (Lee 1974) and prey found in larval cottids from winter and spring 1973 yielded indirect evidence of density-independent foraging among these larvae. Although zooplankton species composition and abundance may vary from year to year, relative constancy has been demonstrated in larval diets of at least two of the five species of cottids in the estuary. Townsend (1981) observed that the principal prey of *M. octodecemspinosus*

(*Microsetella*, *Temora*, and *Balanus* nauplii) and *M. scorpius* larvae (*Balanus* nauplii and *Coscinodiscus*) in the Damariscotta River estuary during winter and spring 1979 were the same as reported from 1973.

Copepods which were relatively abundant during winter and spring months in the Damariscotta River estuary were *Eurytemora herdmani*, *Oithona similis*, and *Pseudocalanus minutus* (Lee 1974). Of these species only *Pseudocalanus* was an important prey of cottid larvae (one species, *Triglops*). *Oithona*, a relatively small cyclopoid, was abundant in early spring but was not eaten by cottid larvae. However, two somewhat larger species were eaten: *Temora longicornis*, whose abundance in winter was variable and lower than in summer and fall, and *Pseudocalanus*. Ivlev (1961) noted that when food is plentiful, fish will take the largest available prey present. But this does not explain why larvae preferentially ate *Temora* and not the same-sized but probably more abundant *Eurytemora* or why they apparently "preferred" the smaller species of pelagic, harpacticoid copepod, *Microsetella norvegica*, over the larger, abundant winter species *Parathalestris croni*. It is perhaps significant that four of the five major prey of *Myoxocephalus* and *Triglops* larvae, *Balanus* nauplii, *Temora*, *Pseudocalanus*, and *Microsetella* were also found to be important natural prey of fish larvae in widely different regions (Lebour 1918, 1919; Sherman and Honey 1971; Arthur 1976; Last 1978a, b). Food selection by fish larvae is controlled by factors such as prey size (the most investigated variable), morphology, catchability (as determined by swimming speeds, escape responses, etc.), and availability (temporal and spatial distribution). None of these factors are well understood.

Most studies of the feeding ecology of fish larvae have focused on prey size, but color (Arthur 1976) and body transparency may also be important cues for "selection" of various copepod prey by fish larvae. All of the harpacticoid copepods ingested by cottid larvae were brightly colored: *Tisbe* spp., red and white stripes; *Zaus* sp., blue-green; *Harpacticus* sp., brown; and *Microsetella*, red. Furthermore, except for *Microsetella*, all are epibenthic forms whose abundance in the water column would not be expected to be high (Noodt 1971). Among the calanoid copepods, differences in body transparency and resulting visibility to predators may explain why *Temora* (which has a dense, thick carapace) was ingested by cottid larvae rather than the more abundant but nearly transparent *Oithona*.

Balanus nauplii, which at times during late winter and early spring can be the most abundant zooplankter in the Damariscotta River estuary (Lee 1974), were the most ubiquitous prey of cottid larvae and appeared to be ingested in direct relation to their abundance in the plankton, i.e., in density-dependent fashion. Comparison of frequencies of occurrence of the six naupliar stages of *Balanus* ingested by *Myoxocephalus* and *Triglops murrayi* larvae in early and late March showed that, with one exception, larvae of all four species caught in early March were feeding solely on naupliar stages 1-3 (Table 14). Later in the month when *Balanus* nauplii became the dominant zooplankter in most ichthyoplankton samples, larvae of all four species (i.e., larvae of varying size and, presumably, prey-catching ability and "preference") were feeding on all six naupliar stages. Percent frequency of occurrence of each stage was remarkably similar among the four cottid species, suggesting that these values might actually reflect relative abundance of each stage in the plankton assuming that each stage is equally susceptible to capture and ingestion. The apparent reliance of cottid larvae on *Balanus* nauplii may be explained by the tendency, observed among adult fishes, to ingest more intermediate-sized rather than larger prey when both are present in abundance (Ivlev 1961; Hyatt 1980). Among larval cottid prey, naupliar

TABLE 14.—Percent frequency of occurrence (%*FO*) of six naupliar stages of *Balanus* spp. (Crisp 1962) in the guts of four species of cottids on (1) 5-6 March and (2) 19-20 March 1973.

Species	*M. aenaeus*		*M. octodecemspinosus*		*M. scorpius*		*T. murrayi*	
Dates	(1)	(2)	(1)	(2)	(1)	(2)	(1)	(2)
No. larvae:	40	78	35	40	33	37	13	23
	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*	%*FO*
Balanus nauplii								
Stage 1	7	5	12	6	6	1	—	3
Stages 2,3	93	52	87	41	91	45	100	45
Stages 4,5	—	31	—	38	0.6	41	—	48
Stage 6	—	5	—	3	—	6	—	2
Stage unknown	0.6	6	2	11	2	7	—	2

stages of *Balanus*, particularly stages 2-4, are somewhat smaller than adult *Temora* and *Pseudocalanus*.

Among fish larvae whose food habits have been reported, cottid larvae most resemble hake (genus *Merluccius*) in prey size at first feeding and in changes of prey size with growth. The first prey ingested by most marine fish larvae range in width from 50 to 100 μm (Houde 1973; Hunter 1980). First prey of hake and cottid larvae are larger: 50-400 μm for *Merluccius productus*; 500 μm mean prey width for *M. merluccius hubbsi*; 100-375 μm for three species of *Myoxocephalus*; and >800 μm for *H. americanus* (Sumida and Moser 1980; de Ciechomski and Weiss 1974). Among fish larvae that ingest 50-100 μm wide prey at first feeding, there is usually a distinct and often dramatic increase in prey size with development. This is seen typically as a change from a diet of copepod eggs and nauplii to one of advanced copepodites and adults. No dramatic increase in prey size or progression in prey types occurs in cottid and hake larvae.

Hunter (1980) recently attempted to categorize marine fish larvae into distinct ecological roles based on those behavioral and physiological traits primarily associated with feeding. Two distinct groups, engrauliform and scombriform, based on extensive field and laboratory observations of northern anchovy and Pacific mackerel larvae, emerged from his analyses. Cottid larvae share some scombriform traits such as relatively large mouths and prey. Similarities in feeding posture, maneuverability, and swimming speed may be inferred because of features in body shape shared by cottid and Pacific mackerel larvae. These larvae, however, would be expected to differ significantly in rates of metabolism and growth because of the different environmental temperature regimes they inhabit: 14°-21°C for highest abundances of Pacific mackerel (Kramer 1960) and 0°-4°C for cottid larvae (Laroche 1980). In this regard, cottid larvae more closely resemble hake larvae which inhabit deeper, colder oceanic waters than either anchovy or Pacific mackerel. Hunter (1980) suggested that hake larvae may belong to a third trophic group characterized by reliance on large prey, a feature already shown to be shared with cottid larvae, and slow metabolism and growth. Although growth rates have not been estimated for cottid larvae, increases in monthly median lengths of ≦1 mm (Laroche 1980) and relatively stationary modes in length-frequency distributions during winter and spring in the Damariscotta River estuary (Townsend 1981) may be explained, in part, by slow growth rates.

Despite some apparent similarities, there are notable differences in the early life histories of hake and the five species of cottids: for example, egg size, 0.98 vs. 1.5-4 mm; size at hatching, 2.4 vs. 5-12 mm; and stage of eye and mouth development at hatching, partial vs. complete. The significance of differences such as these in further distinguishing ecological roles among fish larvae will be better understood only after the early feeding ecology of more species has been investigated.

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FOOD HABITS OF JUVENILE SALMON IN THE OREGON COASTAL ZONE, JUNE 1979

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ABSTRACT

Euphausiids, hyperiid amphipods, crab larvae, and fishes were the important prey identified from stomachs of 408 juvenile salmon collected in a purse seine along the Oregon coast in June 1979. Food habits of juvenile salmon differed among species. About 95% of the weight and numbers of prey of chum salmon consisted of euphausiids and hyperiids. Euphausiids and hyperiids were numerically the most abundant prey items of juvenile coho and chinook salmon, but, on a weight basis, over half the stomach contents consisted of fishes.

Variability in food habits was high for both juvenile coho and chinook salmon. Fishes from only 2 of 45 station pairs (coho) and 3 of 28 (chinook) had diet similarities >75%. The statistical relationship between weight of euphausiids and weight of fishes in stomachs for coho and chinook juveniles showed a strong tendency for both species to contain large amounts of either fishes or euphausiids, but not both simultaneously.

Diet overlap between coho and chinook juveniles was high overall, but low between the same 20 mm size classes of these same species. Euphausiids were eaten in equal numbers throughout the 100-200 mm coho size range; euphausiids were not eaten by chinook <180 mm fork length. Hyperiids were mainly eaten by 180-220 mm coho and by 140-180 mm chinook. Fishes were consumed mainly by juveniles of both species >160 mm.

Based on estimated zooplankton standing stocks, an average (160 mm) coho salmon would have to search and consume all prey in a minimum volume of about 2-8 m^3 per day to fill its stomach. The average abundance of juvenile coho, as determined from purse seining, was 1 smolt per 11,500 m^3, or about 1,440-5,760 times the minimum search volume. These data are related to the question of whether food limitation exists for juvenile salmonids in the sea.

Our knowledge of the ecology of salmon in the ocean, especially during early juvenile life, is scant compared with our understanding of the freshwater phase of salmon life. The first few months that juvenile salmon spend at sea have been identified as a critical period when year-class success may be affected (Gunsolus 1978[3]; Walters et al. 1978; Healey 1980). Basic studies of abundance and distribution, growth, mortality, and feeding habits of young salmon during their first few months at sea are needed to evaluate how the ocean environment and the density of juvenile salmon affect the production of adult salmon.

This paper contributes new information on feeding habits of juveniles of three species of salmon off the Oregon coast: coho, *Oncorhynchus kisutch*; chinook, *O. tshawytscha*; and chum, *O. keta*, salmon. The authors describe the food habits of each species, variability in food habits among fishes collected at different stations, diet overlap between coho and chinook, and speculate on the impact of foraging juvenile coho on zooplankton populations in coastal waters.

METHODS

Fish were collected in a purse seine 457 m long × 30 m deep, constructed of 32 mm stretch mesh with 30 meshes of 127 mm mesh along the bottom of the net. The maximum volume of water encompassed by a round haul set that fished to 10 m depth was calculated to be no more than $1.5 \times 10^5 m^3$. A total of 56 purse seine sets were made between 18 and 29 June 1979 in three regions of the Oregon coastal zone: Off the Columbia River (northern Oregon), off Newport (central Oregon), and in the vicinity of Coos Bay (southern Oregon) (Fig. 1). A total of 509 salmonids <35 cm FL (fork length) (henceforth called juveniles)

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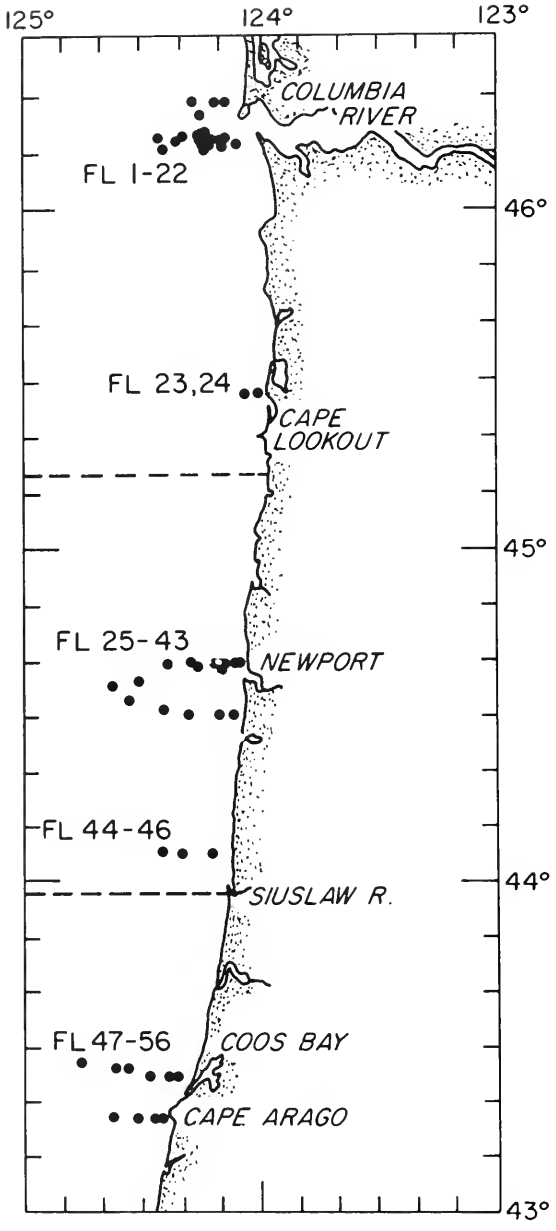

FIGURE 1.—Location of the 56 purse seine sets made by the FV *Flamingo* (FL), 18-29 June 1979. Three geographical regions were arbitrarily defined as northern (FL 1-24), central (FL 25-46), and southern (FL 47-56).

were collected in the sets. Stomach contents of 220 juvenile coho, 147 juvenile chinook, and 41 juvenile chum salmon were examined.

Whole fish <35 cm FL were preserved at sea, after slitting the body cavity, in a 5-15% Formalin[4]-seawater mixture. In the laboratory, all juvenile salmonids were identified to species, measured (fork length), and stomachs removed. Relative stomach fullness was visually estimated on a scale of 0-3 (where 0 = empty; 1, 2, and 3 = fullness in thirds; distended stomachs = 3). State of digestion was noted as one of three subjective categories: Well-digested, partially digested, or fresh. Due to the possibility of differential digestion times of prey items, categorization of state of digestion probably has little meaning except for the "fresh" category.

Food items were identified to the lowest possible taxonomic level and enumerated. Crustaceans and fishes were also identified to developmental stage. Standard length of all fish prey was measured as well as total length of most of the invertebrate taxa from the coho salmon stomachs. Euphausiid lengths were measured from the posterior edge of the eye socket to the tip of the telson. Stomach contents of all salmonids were sorted into major taxonomic groups, damp-dried on absorbent paper, and weighed to the nearest 0.01 g.

RESULTS

Occurrence and Abundances of Prey Taxa

Table 1 lists the average abundances of major taxa of prey in salmonid stomachs and the average length and length ranges of fishes examined. Euphausiids, amphipods, and crab larvae were the most numerous taxa in the stomachs of juveniles of all three species. Fishes were the only other major taxa found in all juvenile salmon. Numbers of fish per stomach were low. On a weight basis, fishes were the most important prey for juvenile coho and chinook, followed by euphausiids (Table 2). Chum stomachs contained mostly euphausiids and amphipods.

Based on percent frequency of occurrence of prey in stomachs, euphausiids occurred in 85% of all chum stomachs, 63% of coho stomachs, and about 50% of chinook and steelhead stomachs (Table 2). Amphipods also ranged in frequency of occurrence from 56 to 32% among these same species. The occurrence of fishes, on the other hand, ranged from 10% of the chum stomachs to 69 and 71% in coho and chinook stomachs, respectively.

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

TABLE 1.—Average number of prey in individual stomachs of juvenile chum, coho, and chinook salmon. A more detailed taxonomic breakdown is given in Table 3.

Prey category	Chum	Coho	Chinook
Euphausiids	44.4	36.9	71.9
Amphipods	30.8	28.0	22.9
Fishes	1.2	4.0	4.2
Crab larvae	2.0	13.5	9.9
Copepods	1.6	6.5	3.2
Molluscs	—	10.6	1.7
Barnacle cyprids	—	4.5	—
Shrimp larvae	—	3.0	1.3
Number of stomachs	41	220	146
Number of empty stomachs	5	22	14
Average length of salmonid (mm)	124	164	208
Range in length (mm)	102-144	94-134	89-308

TABLE 2.—Average wet weight (in grams) of major prey groups found in juvenile chum, coho, and chinook salmon stomachs. Numbers in parentheses are percentages of salmon stomachs containing the specific prey item. Average weight of stomach contents is for fish with food in their stomachs. Weights of salmon are wet weights calculated from mean lengths using the length-weight equations of Healey (1980).

	Chum		Coho		Chinook	
Prey category	Wt.	%	Wt.	%	Wt.	%
Euphausiids	0.22	(85)	0.35	(63)	0.63	(51)
Amphipods	0.04	(56)	0.20	(43)	0.12	(31)
Fishes	0.07	(10)	0.73	(69)	1.04	(71)
All others	0.04	(7)	0.12	(88)	0.46	(70)
Average weight of stomach contents (g)	0.28		0.93		1.30	
Average weight of salmon (g)	23.5		55.3		140.7	
Stomach contents as % body weight	1.2		1.7		0.9	

Total weight of stomach contents of each of the three species of juvenile salmon reflects the size of the fishes sampled (Table 2). Weights of stomach contents expressed as percent of total body weight are similar, however, averaging about 1.3%.

Frequencies of occurrence and average abundances of specific prey taxa for each of the three juvenile salmon are shown in Table 3 and are referred to in the following discussion of the diets for each of the species.

Chum Salmon

The diet of chum salmon consisted mainly of the euphausiid *Thysanoëssa spinifera* and the hyperiid amphipod *Hyperoche medusarum*. Mean numerical abundances of *T. spinifera* per chum stomach collected from northern, central, and southern Oregon were 30.1, 149.7, and 3.7, respectively; abundances of hyperiids were 2.9, 104.8, and 17.5, respectively. Both these prey were most common in chum salmon stomachs collected off central Oregon, but sample sizes were so small that it is difficult to attach any real significance to these differences.

Coho Salmon

A total of 19 invertebrate and 13 fish taxa were identified from coho stomachs (Table 3). Major prey items were juvenile euphausiids (*T. spinifera*, average length about 9.0 mm), unidentified hyperiid amphipods (average length about 4.5 mm), and various fishes (most between 25 and 30 mm long). The most frequently occurring fish identified from the juvenile coho stomachs were Pacific sand lance, *Ammodytes hexapterus*; juvenile rockfishes, *Sebastes* spp.; and larval or juvenile stages of several species of flatfishes, clupeids, and osmerids.

Average length of the prey euphausiid, *T. spinifera*, was directly related to length of the juvenile coho predator. The slope of the regression line (Fig. 2) was significantly different from zero ($r = 0.46$, 28 df, $P \sim 0.01$), indicating that coho between 100 and 210 mm long eat progressively larger euphausiids. Juvenile coho fed on a broad spectrum of fish prey sizes, but, again, larger fish often consumed larger prey. Coho 141-180 mm long fed mainly on fish that were 11-30 mm long, whereas 181-200 mm coho consumed mostly larger fishes, ranging from 21 to 40 mm long (Table 4). However, the regression of lengths of whole prey fishes on lengths of juvenile coho, 94-220 mm, was not significantly different from zero.

Relationships between size of coho and numbers and sizes of prey were studied for 87 juve-

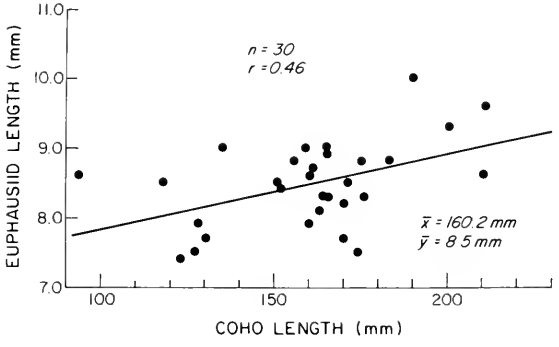

FIGURE 2.—The relationship between coho length and mean euphausiid prey length.

TABLE 3.—Frequency of occurrence (f/n %) and average abundance ($\bar{x}$) of prey found in stomachs of juvenile chum, coho, and chinook salmon.

Prey taxa	Chum		Coho		Chinook	
	f/n %	$\bar{x}$	f/n %	$\bar{x}$	f/n %	$\bar{x}$
Euphausiids						
Thysanoessa spinifera (9 mm)	83	44.1	56	2.0	53	80.9
T. spinifera (22 mm)	2	2.0	15	2.2	5	1.9
Euphausia pacifica (18 mm)	2	1.0	8	2.0	3	14.5
Unidentified	10	12.7			5	4.3
Amphipods						
Parathemisto pacifica	15	1.2			8	1.6
Hyperoche medusarum	34	46.7			20	42.2
Primno macropa					2	1.0
Unidentified Hyperiidae	15	7.8	44	30.1	19	35.7
Gammaridae (*Atylus tridens*)			11	5.0	12	2.1
Fishes						
Ammodytidae						
Ammodytes hexapterus	10	1.2	30	2.4	32	2.0
Pleuronectiformes						
Isopsetta isolepis			1	1.0		
Citharichthys spp.			1	1.3		
Psettichthys melanostictus			1	1.0		
Unidentified flatfish			8	1.8	32	7.8
Hexagrammidae			3	1.6		
Gadidae			1	1.3	2	1.3
Cottidae					11	1.8
Hemilepidotus spp.			3	4.8		
Unidentified			3	1.6		
Clupeidae			6	3.1	3	2.2
Osmeridae			5	3.2	3	3.0
Scorpaenidae						
Sebastes spp.			15	3.5	8	1.4
Unidentified and Digested	10	2.5	45	3.1	48	1.7
Crab Larvae						
Cancer magister megalopae			16	4.2	9	1.8
Cancer spp. megalopae			16	0.6		
Pinnotheridae zoeae			10	4.7	3	19.2
Pinnotheridae megalopae					12	16.2
Paguridae zoeae					3	2.0
Copepods						
Calanus cristatus			6	8.1	1	12.0
C. marshallae			4	2.0		
Eucalanus bungii			4	1.0		
Epilabidocera longipedata			1	1.0		
Unidentified	12	1.6			3	1.0
Molluscs						
Limacina helicina			7	10.6	2	1.7
Cephalopods					1	1.0
Miscellaneous Arthropods						
Juvenile Crabs					4	14.0
Decapod shrimp mysis	2	2.0	6	2.5	6	1.0
Pandalus jordani zoeae			4	1.0	3	1.3
Barnacle cyprids	2	1.0	7	4.4		
Mysids			3	1.2	2	1.3
Insects	2	1.0	2	1.2	1	1.0
Chaetognatha						
Sagitta elegans	2	5.0	1	1.0		
Polychaetes						
Tomopteris sp.			1	6.5		

TABLE 4.—Frequency distribution of lengths of fish prey found in stomachs of juvenile coho salmon of various lengths.

Standard length of coho (mm)	Number of coho	Length of fish prey (mm)						
		0-10	11-20	21-30	31-40	41-50	51-60	>60
81-100	1		1	1				
101-120	3		3	1				
121-140	36	3	7	10	1	4		
141-160	66		27	35	4	4	1	1
161-180	70	8	69	80	28	21	2	
181-200	30		5	25	23	3	4	
201-220	7			7		1	1	

nile coho with stomachs full of fresh material to minimize the problem of differential digestion rates of various prey items. No statistically significant differences ($P>0.05$) were found between length of coho and either number of euphausiids, total number of prey items, or num-

bers of fishes. Significantly greater numbers of hyperiid amphipods occurred, however, in larger than in smaller coho (Fig. 3). Average weight of fishes in stomachs also increased with length of juvenile coho. Total weight of stomach contents was related to length of juvenile coho (weight of prey $= -1.0 + 0.016 \times$ length of coho, $r = 0.43$, $P<0.01$). The relationship between the two food groups most important to juvenile coho was investigated by plotting weights of euphausiids versus weights of fishes in the stomachs for each of the 87 coho. This plot was divided into quadrants by drawing lines parallel to the abscissa and ordinate at the median values of euphausiid and fish weight. The numbers of data points in each quadrant are shown in a 2×2 contingency table (Table 5). The χ^2 of 12.5 was highly significant ($P<0.01$, 1 df), indicating a strong tendency for juvenile coho to contain large amounts by weight of either fishes or euphausiids, but not both at the same time. Of these 87 coho, 26% contained only fishes and 21% only euphausiids. This trend may be a result of active selection of one type of prey or a result of prey patchiness. The latter explanation may be more plausible, since stratification of these two prey groups in the stomachs was evident in those individuals containing both prey items.

TABLE 5.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 87 juvenile coho salmon.

		Euphausiid prey (g)	
		<0.24	>0.24
Fish prey (g)	>0.48	31	13
	<0.48	13	30

Variability in the composition of stomach contents of coho salmon was often high among the 10 stations where at least six fish were analyzed per station (Table 6). For example, juvenile euphausiids were the most numerically abundant prey taxa at four stations (2, 3, 12, and 29); hyperiid amphipods at four other stations (10, 27, 28, and 39); and fishes and crab larvae at one station each. The differences in feeding habits among stations were compared by calculating similarity indices for all possible station pairs. We used the percent similarity index (PSI $= \Sigma \min P_i$), where

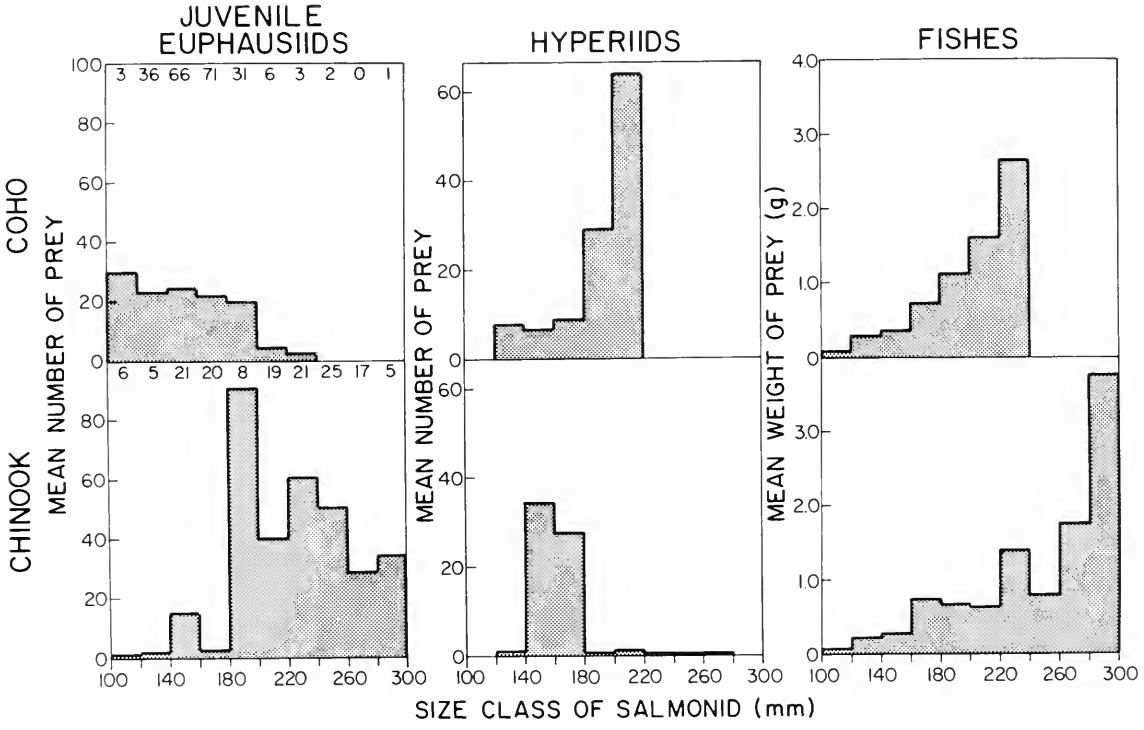

FIGURE 3.—Average abundance of juvenile euphausiids and hyperiids and average weight of fish prey occurring in the stomachs of each 20 mm size class of juvenile coho and chinook salmon. The averages are taken over only those stomachs in which prey items occurred. The numbers at the top of the leftmost figure denote the sample size in each 20 mm size class.

TABLE 6.—Sampling data and percent of total numbers of major prey items found in juvenile coho stomachs off the Oregon coast (only at those stations where six or more juvenile coho were taken). Includes only those prey taxa comprising 2% or more of the total number of prey items.

	Northern Oregon						Central Oregon			
Station	1	2	3	10	12	22	27	28	29	39
Time of day	0630	0900	1000	1730	0800	1500	0930	1130	1300	0900
Day in June	18	18	18	19	20	21	23	23	23	27
Water depth (m)	40	77	102	66	77	130	55	77	73	55
Distance from shore (km)	11.8	19.4	25.9	13.3	19.1	33.3	10.0	16.3	27.0	9.4
Number of coho examined	33	14	16	32	37	30	8	6	11	8
Average length of coho (mm)	158	175	158	154	158	163	165	161	157	193
Percent of coho with empty or nearly empty stomachs	58	79	69	25	8	20	12	33	0	0
Thysanoëssa spinifera (juveniles)	8.9	68.3	41.4	6.3	93.4	12.1	9.8	2.6	53.5	3.4
Hyperiid amphipods	20.1	22.5	26.9	36.0		13.0	39.7	89.9	30.7	94.0
Fishes	42.0	2.9	8.4	10.7	6.0	8.4	29.3			
Crab megalops				16.5		26.1				
Crab zoea			4.0			24.0				
Pteropods									9.2	
Calanus cristatus							6.5		4.9	
Cancer magister megalops			4.9	17.0		4.9				
Gammarid amphipods			6.2			7.7				
T. spinifera (adult)	16.6	2.1								
Barnacle cyprids			3.1	9.3		2.2				
Euphausia pacifica	9 5		3.1							
Total number of prey items	169	378	227	364	2,516	1,135	174	306	1,745	1,326

P_i is the proportion of the ith taxa (based on numbers of individual prey) in a stomach (Whittaker 1960), and PSI between a pair of stations is calculated by summing the smaller (minimum) P_i's for all food items. Similarity was generally low (<50%) among stations. Only 6 of the 45 possible pairings showed similarities >66% (stations 2-3, 2-12, 2-29, 3-29, 10-27, and 28-39), and only two pairs had a similarity >75% (2-29 and 28-39).

Some of this variability among stations may be related to the geographical regions sampled. For example, the numerical percentage of euphausiids averaged 45.5% for coho caught near the Columbia River plume (stations 1-22) compared with 17.4% off the central Oregon coast (stations 27-39, Table 6). Fishes occurred in the diets at all stations and made up 14% of the total prey numbers in the Columbia River area, whereas they were a significant part of coho diets at only one of four stations off Newport. Amphipods occurred more frequently in the stomach contents off Newport, averaging 63.6% of the total number, compared with 20.1% in coho from the Columbia River plume. The copepod, *Calanus cristatus*, and pteropod, *Limacina helicina*, were important components of the diets of only those juvenile coho caught off the central Oregon coast. An additional component of among-station variability may be attributed to differences in diet between inshore and offshore stations. Coho taken within 12 km of shore contained a greater proportion of fishes at two of three stations, while those captured offshore contained more euphausiids.

Chinook Salmon

Thirty taxa were identified from the stomachs of juvenile chinook. Major prey items were juvenile euphausiids (*T. spinifera*), hyperiid amphipods (mostly *Hyperoche medusarum*), pinnotherid crab larvae, and various fishes (Table 3). The most frequently identified fishes were flatfish and Pacific sand lance larvae, both occurring in 31% of the stomachs. Juvenile scorpaenids were third, occurring in only 7% of the stomachs.

Chinook salmon with stomachs full of fresh food ($n = 42$) were studied to test the hypothesis that weight of euphausiids and weight of fish prey in stomachs were independent, using the same procedure as with coho. The χ^2 from the contingency table (Table 7) was significant at the 0.07 level. Hence there is a tendency for chinook to eat either euphausiids or fishes, but this inverse relationship is not as strong as for juvenile coho salmon. The weight of stomach contents increased with size of juvenile chinook salmon. The slope of the regression (weight of prey = $-4.2 + 0.032 \times$ length of chinook, over the range of 100-200 mm) was significantly different from zero ($r = 0.66$, $P<0.05$).

TABLE 7.—Contingency table comparing weight of fish and euphausiid prey found in the stomachs of 42 juvenile chinook salmon.

		Euphausiid prey (g)	
		= 0.0	>0.0
Fish prey (g)	>0.67	14	7
	<0.67	7	14

Based on the percent by number, euphausiids and fishes were more important in the diet of chinook collected off the Columbia River than off the central Oregon coast (Table 8). As with coho, between-station variability was high. Only three station pairs had high similarities in diet (PSI >90%: 11-12, 11-14, and 12-14) mainly due to the high proportions of *T. spinifera* consumed at these stations.

Diet Overlap

Similarity (PSI) was calculated as before to study diet overlap among species of juvenile salmon at four stations where at least eight individuals of two or more salmon species occurred. Diets were similar (PSI >66%) at three of these stations. At station 12, chum, coho, and chinook juveniles ate 94.7, 93.4, and 90.9% euphausiids, respectively, by number; at station 27, coho and chinook ate nearly equal proportions of hyperiids and fishes; and at station 39, coho and chinook ate 94.0 and 91.3% hyperiids, respectively. Diets were dissimilar at station 1.

This dietary overlap among cooccurring species of juvenile salmonids suggests that a potential exists for competition, should food be limiting. This potential was highest among different size classes of juvenile coho and chinook salmon but was reduced among similar-sized fishes (Fig. 3). Euphausiids were eaten most often by coho 100-200 mm long, but not by chinook <180 mm. The opposite pattern is seen with hyperiid amphipods: Small chinook (<180 mm) ate more hyperiids than similar-sized coho. As juvenile salmonids of both species increased in length, they consumed larger fish, but coho between 140 and 330 mm consumed larger fish on the average than chinook of the same size. Juvenile chinook also consumed more pleuronectid larvae and fewer scorpaenids than coho. Chinook ate very few pteropods and no barnacle cyprids while these taxa occurred in about 10% of the coho stomachs (Table 3).

DISCUSSION

Fishes, euphausiids, hyperiid amphipods, and crab larvae were the most important prey for juvenile salmon off Oregon. Other published studies dealing with the diet of juvenile salmonids in the ocean show basically the same result, although there are notable differences. Manzer (1969) concluded that juvenile chum salmon from Chatham Sound, British Columbia, were planktivorous, feeding mostly on larvaceans (*Oikopleura* spp.) and unidentified copepods, and that coho were piscivorous, feeding mostly on Pacific herring and sand lance. Healey (1980) found that juvenile chum salmon from Saanich Inlet also fed predominantly on larvaceans and copepods, but individuals caught in more open waters of Georgia Strait ate euphausiids, amphipods, and fishes, as found off Oregon in this study. Juvenile coho studied by Healey contained 34% fishes (by volume) in Georgia Strait and 3% in Saanich Inlet, appreciably less than the 70% reported by Manzer in Chatham Sound. Healey concluded that chinook and coho from Georgia Strait had very similar food habits. Fresh et al.

TABLE 8.—Sampling data and percent of total numbers of major prey items found in juvenile chinook stomachs off the Oregon coast (only at those stations where six or more individual chinook were taken). Includes only those prey taxa comprising at least 2% of the total number of prey items.

	Northern Oregon						Central Oregon		
Station	1	8	11	12	14	18	27	39	43
Time of day	0630	1415	1915	0800	1055	1000	0930	0900	0410
Day in June	18	19	19	20	20	21	23	27	28
Water depth (m)	40	38	68	77	71	73	55	55	57
Distance from shore (km)	11.8	11.1	17.2	19.1	18.9	17.6	10.0	9.4	9.3
Number of chinook examined	8	9	12	14	13	14	19	11	6
Average length of chinook (mm)	147	208	239	253	211	245	183	164	178
Percent of chinook with empty or nearly empty stomachs	50	11	8	36	15	29	47	27	17
Thysanoëssa spinifera (juveniles)			97.2	90.9	98.9	22.8			46.4
Hyperiid amphipods		68.1				5.4	37.8	91.3	23.7
Fishes	30.1	25.3		8.3		45.7	19.9		13.4
Crab megalops	2.5	2.1				10.9	7.9	7.5	
Pteropods							31.6		
Euphausia pacifica	61.5								
T. spinifera (adults)	2.5					4.3			
Atylus tridens		2.1				3.2			
Calanus cristatus									12.4
Unidentified items	2.5								
Total number of prey items	39	185	1,906	277	1,846	92	291	987	97

(1981) reported that juvenile chum from nearshore pelagic habitats of Puget Sound fed on euphausiids, crab larvae, and gammarid amphipods on a weight basis; coho fed largely on larvae of decapod crustaceans; and chinook fed on euphausiids.

The qualitative range in variability of diet present during our 2-wk sampling period was similar to that found by the above authors from various months, years, and geographical locations. At some times and locations, euphausiids were dominant prey; at others, amphipods and fishes. This variability suggests that juvenile salmon are opportunistic, feeding on abundant prey available at a particular time and place.

The main prey items of our juvenile salmon comprise three general size groups: 1) Fishes having an average length of 29 mm, 2) euphausiids and *Cancer magister* megalopae, ranging in length from 7 to 10 mm, and 3) hyperiid amphipods between 4 and 6 mm.The fact that juvenile salmonids ate large numbers of euphausiids agrees with what is known about the abundances of various-sized planktonic prey sampled in coastal waters of Oregon during period years (Table 9). Over the range of 7-10 mm, euphausiids were the most abundant prey item. Shrimp larvae and *C. magister* megalopae were abundant only during limited periods, usually only June.

The predominant euphausiid eaten was *T. spinifera*, a neritic species. *Euphausia pacifica*, although a more abundant species of euphausiid in the North Pacific, is more oceanic and is not common in shallow shelf waters (Hebard 1966; Peterson and Miller 1976; Youngbluth 1976) and was found in low numbers in our salmonid stomachs. Juvenile salmonids collected off Oregon fed predominantly on subadult individuals, possibly because adult euphausiids migrate into deeper waters during the day (Alton and Blackburn 1972) when salmon presumably feed. Subadult euphausiids are abundant in the upper 20 m of the water column during both day and night (Peterson[5]).

The large numbers of hyperiid amphipods and the paucity of copepods in the diet of juvenile salmon were surprising. Hyperiids are neither abundant in Oregon coastal waters nor are they particularly large compared with other more common planktonic taxa (Table 9). The average length of the amphipods (4.5 mm) is not much greater than *Calanus marshallae* (stage 5 copepodites and females, 3.0-4.0 mm TL (total length)). The ratio of amphipods to C5 *C. marshallae* abundance was 1:14 in plankton samples (Table 9) but 4:1 in the stomachs of juvenile coho. Frequency of occurrence in juvenile coho stomachs was 44% for amphipods compared with only 6% for *Calanus*. Similarly, the copepod *C. cristatus* (8 mm TL), with an average abundance about the same as hyperiids, was seldom eaten. Length alone may not be adequate for assessing size-selective predation in juvenile salmon. Okada and Taniguchi (1971) found that the upper size limit of prey may be determined by prey width. This may be relevant because hyperiids are generally much broader at their widest dimension than copepods of the same length.

One hypothesis to explain the high selectivity of amphipods by juvenile coho salmon concerns their peculiar swimming behavior and pigmentation. In the laboratory, hyperiids caught in coastal waters were extremely active swimmers (Peterson[6]). Most species have a large, heavily pigmented (black) compound eye, which could increase their detection by a visual predator, as shown for freshwater fish (Zaret and Kerfoot 1975). Copepods, on the other hand, lack the visual contrast of amphipods and are less active swimmers, generally swimming upwards and

TABLE 9.—Abundance of salmonid prey averaged from plankton samples collected during June and July at stations located 1, 3, 5, and 10 mi off Newport, Oreg. Zooplankton are averaged over the years 1969-72 (Peterson and Miller 1976); crab larvae over the years 1969-71 (Lough 1975, 1976); and larval fish from 1971 only (Richardson and Pearcy 1977). Plankton tows are step-oblique through the entire water column, during daytime, using a 0.2 m diameter bongo net (0.24 mm mesh) for zooplankton and a 0.7 m bongo net (0.5 mm mesh) for fish larvae.

Prey taxa	Average no./m^3
Pinnotheridae megalopae	0.1-1
Cancer magister megalopae	1-8
Pagurus megalopae	10-20
Calanus cristatus	2.3
C. marshallae (C5 + females)	50
Pteropods	14.3
Hyperiid amphipods	3.6
Decapod shrimp mysis	19.2
Chaetognaths	11.7
Thysanoëssa spinifera	6.8
Larval fish	1-2

[5]W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, unpubl. data, 1977.

[6]W. T. Peterson, Marine Sciences Research Center, State University of New York-Stony Brook, Stony Brook, NY 11794, pers. obs. 1978.

then sinking passively through a portion of the water column.

Another explanation for the presence of large numbers of hyperiids in salmonid guts is that juvenile salmon may pick them from the surface of medusae. The predominant hyperiid consumed by chinook and chum salmon was *Hyperoche medusarum*, a species known to live on the exumbrellar surface of medusae (Bowman et al. 1963; Harbison et al. 1977). The host may be easy for salmon to locate, particularly the large *Chrysaora fuscescens* (bell diameter of several tens of centimeters), which were very numerous in our purse seine samples.

Larval fishes were the other important prey item. Information on their distribution and abundance is limited to sampling done in 1971-72. Data given in Table 9 are from Richardson and Pearcy (1977) for larvae captured at stations within 2-28 km from shore. Abundances were 200-400 larvae/10 m^2, or 1-2 larvae/m^3, assuming they are all distributed only within the upper 20 m of the water column.

To investigate the question of food limitation, estimates are needed of salmonid feeding rates, salmonid abundance, prey abundance, and prey population growth rates. Feeding and digestive rates can be inferred from field data, if there is pronounced diel periodicity in stomach fullness or state of digestion (Eggers 1977; Lane et al. 1979), but we have no evidence for this in our limited study. Thus, whereas estimates of stomach fullness were obtained from this study, feeding rates were estimated from other studies. The average weight of food in full juvenile coho stomachs (1.5 g wet weight) is equivalent to about 2.6% of the 55 g body weight of an average juvenile coho (160 mm long) (from Healey 1980). Walters et al. (1978, fig. 6) showed that the maximum ration of juvenile sockeye salmon weighing 55 g is slightly <3% of body weight per day. On the other hand, Brett (1971) found that the maximum daily intake of food was 7-8% of body weight for a 50 g sockeye salmon. Therefore, we assume that juvenile coho fill their stomachs between 1 and 3 times per day on the average.

Averaged over the 2-wk period in June 1979, the average 160 mm juvenile coho contained 37 euphausiids, 28 amphipods, and 4 fish (Table 1). In order to locate this quantity of food, this salmon would have had to search a minimum of approximately 5.4 m^3 of water for the euphausiids, 7.8 m^3 for the amphipods, and at least 4.0 m^3 for the larval fish. This assumes that all prey available to plankton nets are also fully available to juvenile salmon, and that annual differences are minor. Considering the well-known problems of zooplankton sampling variability and the fact that samples from different years are being compared, the agreement on water volume searched by salmon to locate each prey item seems quite good.

The maximum abundance of juvenile salmonids in any one purse seine was 123 fish, and the average number of fish in sets in which at least 5 fish were caught was 26. The mean abundance in these 16 sets was 17 fish/$10^5 m^3$. Juvenile coho abundances were about one-half as great, 8.7 fish/$10^5 m^3$, or 1 fish/11,500 m^3. If a juvenile coho fills its gut once per day, it needs to eat all prey in about 4-8 m^3 water/d. Thus, as a rough average, one individual would consume at least 4/11,500-8/11,500 (or 0.03-0.07%) of the available prey per day. Should this individual coho fill its gut three times each day, it would consume up to 0.1-0.2% of the standing stock of prey per day. Coho and chinook combined would consume about 0.2-0.4% of available prey per day. If growth rates of prey population equal or exceed these loss rates, predation by juvenile coho and chinook alone will not reduce standing stocks of prey. Unfortunately, estimates of these vital parameters are lacking.

Walters et al. (1978) examined the effect of food limitation on juvenile salmon growth and survival using a computer simulation model. Input variables included 1) zooplankton distribution, abundance, and production rates; 2) ration, growth, and mortality of young salmon in relation to body size; and 3) timing of arrival of smolts at sea and rate of migration along the coast in relation to zooplankton production cycles. They tentatively concluded that juvenile salmonids were not food-limited, but rather predator-limited. This conclusion rests on a crucial assumption of the availability of zooplankton prey, which may be in error. Their estimates of zooplankton production and mortality and fish consumption (their table 3, columns 5, 6, and 7) were calculated using estimates of the biomass of zooplankton within a 20-400 m water column, despite their assumption that salmon forage only in the upper 20 m of the water column. They assumed that zooplankton prey removed by salmon during the day will be replaced from deepwater zooplankton populations at night. Since the surface biomass is enhanced by diel vertical migrations mainly at night and juvenile salmonids are

thought to be daylight or crepuscular feeders (see Bailey et al. 1975; Godin 1981 and references therein), they may never encounter this nighttime increase in zooplankton abundance.

The studies of Healey (1980) and Simenstad et al. (1980[7]) both suggest that food availability may affect the abundance of juvenile salmon. They found that fewer salmon remained in Georgia Strait (British Columbia) and Hood Canal (Washington), respectively, when feeding conditions were poor. Obviously, the question of ocean limitation of salmon production cannot be resolved until much more is learned about the ecology of juvenile salmon and their competitors in the coastal zone. Substantially more information is needed on the abundance and availability of prey in near-surface waters, as well as on feeding, growth rates, and migration patterns of juvenile salmon.

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SPAWNING AND LARVAL DEVELOPMENT OF THE HOGFISH, *LACHNOLAIMUS MAXIMUS* (PISCES: LABRIDAE)

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ABSTRACT

Spawning of the hogfish, *Lachnolaimus maximus*, along a reef-sand interface near the insular shelf edge off southwestern Puerto Rico was observed over a period of 20 months by scuba diving. Eggs were collected and returned to the laboratory for hatching. Male-female ratio was about 1:10. Males patrolled elongate territories, which did not change during the 20 months, during the afternoon. Males initiated spawning by a courtship display using the prolonged dorsal fin spines and other fins. If the female responded, an elaborate process, termed the spawning rush, occurred during which the gametes were released. A male spawned with one female at a time, but often spawned with several females during an afternoon. Peak spawning was from December to April. There was no evidence that spawning was influenced by current speed or direction or by lunar or tidal periodicity. Eggs were planktonic, about 1.2 mm in diameter, lacked visible pigment, and hatched in 23 hours at 25.5°C. They were preyed on extensively by yellowtail snappers, *Ocyurus chrysurus*. Larvae, which survived in the laboratory up to 50 days, lacked a distinct transformation to juveniles but gradually acquired pigment and juvenile form after 13 days. Free-swimming postlarvae formed mucous bubbles at night.

The hogfish, *Lachnolaimus maximus* (Walbaum), is the largest tropical western Atlantic labrid, reaching about 11 kg (Randall and Warmke 1967); adults are conspicuous members of many reef communities. A highly prized foodfish, it is taken incidentally with other fishes, particularly by spear or hook and line.

It is a protogynous hermaphrodite, but there are no primary males. Color patterns are distinctive between sexes. Males, which are more highly pigmented, have a dark reddish brown mask on the head. Also of the same hue are the base and first soft rays of the dorsal fin, the base of the rays in the lunate caudal fin, the pelvic fins, and the leading edge of the anal fin. The color of these darkened areas varies in intensity, depending on the nervous state of the male. The pectoral fins are yellow and there is an elongate spot on each side of the body. Females lack the reddish brown darkening, but possess a black spot about the size of the eye at the posterior base of the dorsal fin. The first three dorsal fin spines are greatly prolonged in males, much more than in females. Males also have filaments on the anal fin, soft dorsal fin, and margins of the caudal fin. The snout is longer in males and has a concave profile.

Although various aspects of its biology, such as food habits (Reid 1954; Randall and Warmke 1967; Davis 1976) and growth (Davis 1976), have been well documented, little has been published on spawning or early life history. While scuba diving on a shelf-edge coral reef off southwestern Puerto Rico to study reef fish spawning, I encountered a large spawning population of hogfish. I was able to observe the courtship display and spawning rush over a 20-mo period from December 1977 to July 1979. I also was able to collect large numbers of fertilized eggs, which were returned to the laboratory and hatched. A large number of larvae were kept alive up to 30 d, while smaller numbers were maintained to 50 d. I was able, therefore, to describe and illustrate in some detail the development of larvae from hatching through the juvenile stage.

METHODS

Observations of Courtship and Spawning

The site was visited 154 d during the 20 mo. From December through March, when spawning was high, visits were daily, if possible, but during the summer, visits were usually weekly.

Males and females were observed both at close range and also from the maximum distances possible. The presence of observers had less effect on

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the behavior of males than females, but no disturbance was noted if the observer moved no closer than about 4-8 m. Only during early phases of the spawning rush would rapid movements by a diver cause the female to abort the spawning rush. Once the spawning rush had reached an advanced point, however, the observer could approach quickly without interrupting. Fish frequently observed seemed to become accustomed to the observers.

Motion pictures (16 mm) were made of different aspects of spawning behavior. These were analyzed frame-by-frame to determine the duration of each act and the orientation of the fish during the rapid spawning rush.

Collection and Rearing of Eggs

Eggs were collected with fine mesh dip nets (sold as "brine shrimp nets") 10 by 15 cm with mesh openings of about 100 μ in diameter. After some practice, an observer could follow a pair on their spawning run and quickly locate the diffuse cloud of gametes when they were released. The cloud was either constantly observed or squirted with ink mixed with seawater from a plastic bottle to provide a reference mark. About 45 s to 1 min were needed to assure fertilization. After that time, eggs were collected by passing the net through the water where the eggs occurred. In one smooth motion, the net was then everted into a plastic bag and the bag was filled with water from the area where the gametes occurred, in hope of obtaining more sperm in the water and thereby increasing the chances of fertilization. Eggs collected before 45 s had elapsed generally were not fertile. Since the ability to see the cloud of gametes decreases with each second, the collection of planktonic eggs with a small hand net is a contest between the time required for fertilization and the ability of the collector to discern the location of the eggs. Although the ink helps to locate the eggs, it quickly disperses or tends to rise or sink because of the differences in density. I found it valuable to remain about 0.5-1.0 m away from the cloud, once it had been located, and focus on sediment particles, opaque eggs, or larger zooplankton rather than trying to follow the rapidly dispersing cloud. If the bag is clear plastic, the eggs, once inside, can be seen easily. It helps to face the sun (underwater) and backlight the eggs by blocking out the sun directly to the eyes with a hand behind the bag.

The eggs in the bags were transported to the laboratory in buckets partially filled with seawater, and were released into aerated closed-circuit 80 l aquaria within about 90 min of being collected. Rearing methods followed Houde and Tanaguchi (1977). The aquarium was constantly illuminated by a twin 20-watt fluorescent lamp. A culture of *Chlorella* was introduced at hatching. Later larvae were fed wild zooplankton collected with 53 μ mesh nets. Temperatures were maintained at 25°-27°C.

Selected eggs and larvae were preserved in 3% Formalin[2]. Larvae were illustrated from preserved specimens by a camera lucida attachment on a dissecting microscope.

The Study Site

The study site was located on the insular shelf edge 16 km ESE of La Parguera, Puerto Rico (approximate position: lat. 17°54'N, long. 66°57'W). It is typical of most reefs off the south coast of Puerto Rico and the Virgin Islands (MacIntyre 1972; Adey et al. 1977). It is an elevated ridge about 100-150 m wide, paralleling the actual shelf break, and has a rocky substrate with abundant coral, particularly on the seaward and inshore flanks. Minimum depth is about 16 m. Near the study area the seaward portion slopes gently to about 18-19 m depth, then plunges downward at an angle of about 60° to oceanic depths. The inshore side slopes downward at about 10° until it meets a nearly level sandy-rubble plain. This slope, termed the "moat slope," is where most spawning activity by *L. maximus* was observed.

Water temperatures varied between 24° and 27°C, visibility between 50 and 10 m. The area is within the trade wind belt of the Atlantic tropics and is consistently exposed to easterly winds of moderate force (Glynn 1973). Waves usually consisted of a small wind produced chop associated with larger swells. Wave heights of 1-2 m were common, but seldom exceeded 2 m. Complete calms would occasionally occur, most often during winter. These calms were associated with lee-shore conditions on the southwestern coast and occurred only a few percent of the time. Currents were generally east to west, paralleling the shelf edge, but occasionally they were completely reversed or ran strongly off or onto the shelf. Clearest water occurred when strong southeast-

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

erly winds drove oceanic water up onto the shelf edge and also produced rough conditions. The most turbid water was either associated with calms, when the normal wind-driven flow from offshore was eliminated, or when large amounts of rain fell on Puerto Rico, particularly during the summer-fall wet season.

OBSERVATIONS

Spawning Groups of *L. maximus*

Males established a territory along the moat-moat slope interface and defended it against the intrusion of other males. The territory was unusual in being very elongate along the moat-moat slope axis, but not ranging far either over the sandy moat or up the moat slope. Males patrolled their territory during the afternoon, passing from one extreme of the sand-reef border to the other without changing direction except as interrupted by spawning rushes with females. Three territories that I closely examined each encompassed about 100 m of the moat-moat slope interface. The turning points at either end remained consistent over the entire 20 mo. During active spawning periods, generally 2-3 min, were required for one "pass" if no spawning occurred.

An estimated 10-15 females occurred with each male during the afternoon. Although I found some evidence that females may remain with the same male during any one day, I could not determine if they changed males at other times.

Time and Conditions of Spawning

Active spawning was observed from December through April, but I could not be sure if spawning also occurred in other months when low water visibility often made observations difficult. Males, however, continued to patrol their territories during the afternoon and were occasionally seen to court females, but no spawning was seen. In any event, it is certain from direct observation that spawning during winter and spring must be at least an order of magnitude above any that may occur during summer and fall. Davis (1976) reported that peak spawning, based on gonad indices, of Florida Keys hogfish is probably in February and March, although some spawning may be occurring in other months. Gonad indices were consistently low from May through August.

There is no evidence for lunar periodicity. During peak spawning periods, spawning rushes occurred on all phases of the moon and spawning proceeded day after day with no apparent change over the lunar cycle.

Spawning began in midafternoon, but the exact time of initiation was never observed. Hogfish were spawning by 1.5 h before sunset and continued to spawn until 15-30 min before sunset. Males began to patrol more slowly as sunset approached, and the frequency of spawning rushes decreased quickly. Females seemed to leave the spawning area, or at least were not visible, by about 15 min before sunset. Males continued to patrol slowly until about sunset, then left the immediate area of the sand-reef interface.

During the season of active spawning, current speed or direction, surge on the bottom, and water clarity seemed to have little effect on spawning behavior. Rushes were observed under nearly all conditions encountered. Water temperatures ranged between 24° and 26°C. Day length was short, being near the annual minimum of about 11 h near the start of peak spawning in December and about 12.5 h by April.

Spawning Behavior

A female often indicated her readiness to spawn by moving up in the water column on approach of a male; otherwise, a male would actively court females encountered on his patrol. If a female was seen near the bottom, a male would swim quickly towards her, shifting from pectoral sculling to caudal fin swimming in a burst of speed, and then dive towards her exhibiting a courtship display. This consisted of erecting the three long anterior spines of the dorsal fin and shaking the posterior two of these rapidly back and forth at about 8-10 cycles/s. The posterior portion of the dorsal fin, the upper and lower caudal fin margins, and the pelvin fins were also agitated at a similar rate. Often the male would swoop above the female and dive rapidly towards her while displaying. If no response was elicited, the male would move quickly on to another female or resume patrolling.

The spawning act was part of an elaborate process termed the spawning rush, which could be initiated by the male actively courting the female or by the female simply rising up in the water column as the male approached on his patrol. The rush required 10-25 s total time from the time the fish left the vicinity of the substrate.

On the basis of hundreds of observations and the complete filming of 12 rushes, the spawning rush may be broken down into six distinct periods: 1) Pectoral swim up, 2) tail swim, 3) swim alongside and tilt, 4) release, 5) circle and display, and 6) swim down (Fig. 1).

1) Pectoral swim up—A male approaching from some distance a female which was up above the bottom would swim upward at an angle of 10°-20° towards the female, using concurrent sculling of the pectoral fins, usually of 2.0-2.5 beats/s. The dorsal and anal fins were folded against the body. As he approached the female, who rose slowly at a steeper angle to match his ascent, the male began to turn laterally and shifted to the second type of swimming.

2) Tail swim—The male folded the pectoral fins against his body and began undulating the caudal fin and posterior portion of his body at about 4 beats/s. Pelvic fins were usually about one-half extended. The female continued to rise slowly as the male approached her from behind. This stage lasted about 2-5 s.

3) Swim alongside and tilt—The male, using the tail only, continued swimming and came forward alongside the female, who was still moving forward. Their bodies were close together, the male slightly behind the female with his snout about even with her eye (Fig. 2). Once alongside, the male angled the dorsal portion of his body outward at about 15°-20° from the female. This took 0.5-1.5 s. During this phase, the male and female turned laterally 90°-180° in the direction of the female.

4) Release—At the end of the turn to initiate gamete release, the male started swimming forward more rapidly than the female. As he overtook her, he bent his body laterally towards her, then broke in the opposite direction. At this time the gametes of both sexes appeared to be released. The cloud could usually be seen, but the exact moment of release was difficult to determine. In some cases the male, when he turned toward the female, was sufficiently far forward to actually cross slightly into her path. The sharp break away from the female was accomplished by a sharp flick of the caudal fin. This also served

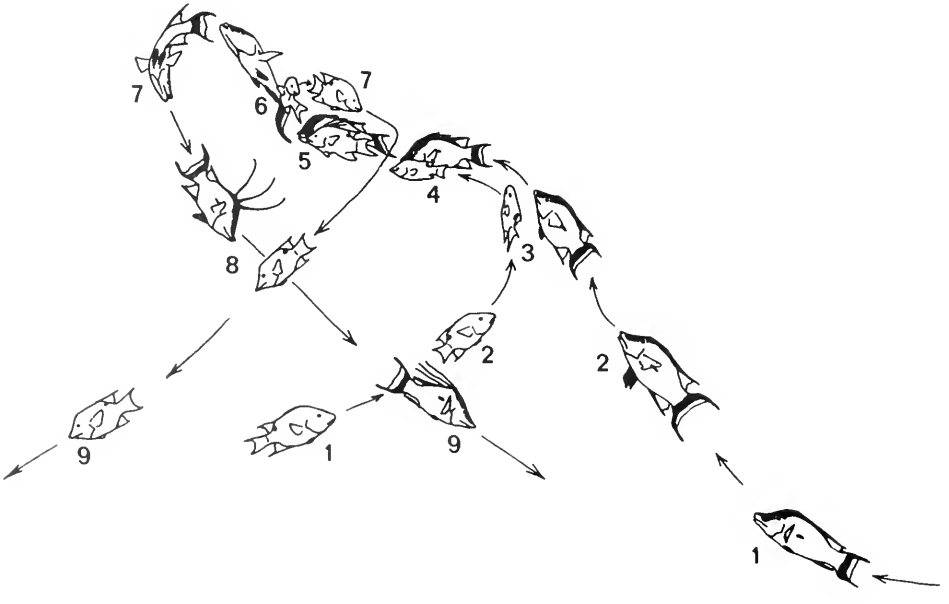

FIGURE 1.—Idealized spawning sequence of *Lachnolaimus maximus* under conditions where the female meets the male in midwater. The male (right) approaches and initiates the "pectoral swim up" action (1) followed by "tail swim" (2-3) when approaching the female. The lateral turn in "swim alongside and tilt" towards the female (4-5) is followed by the "release" of the gametes (6). "Circle and display" (7-8) precedes "swim down" (9). In this case the male is illustrated as returning in the direction opposite that when spawning was initiated, but this is not always the case. Often the male will continue patrolling in the same direction.

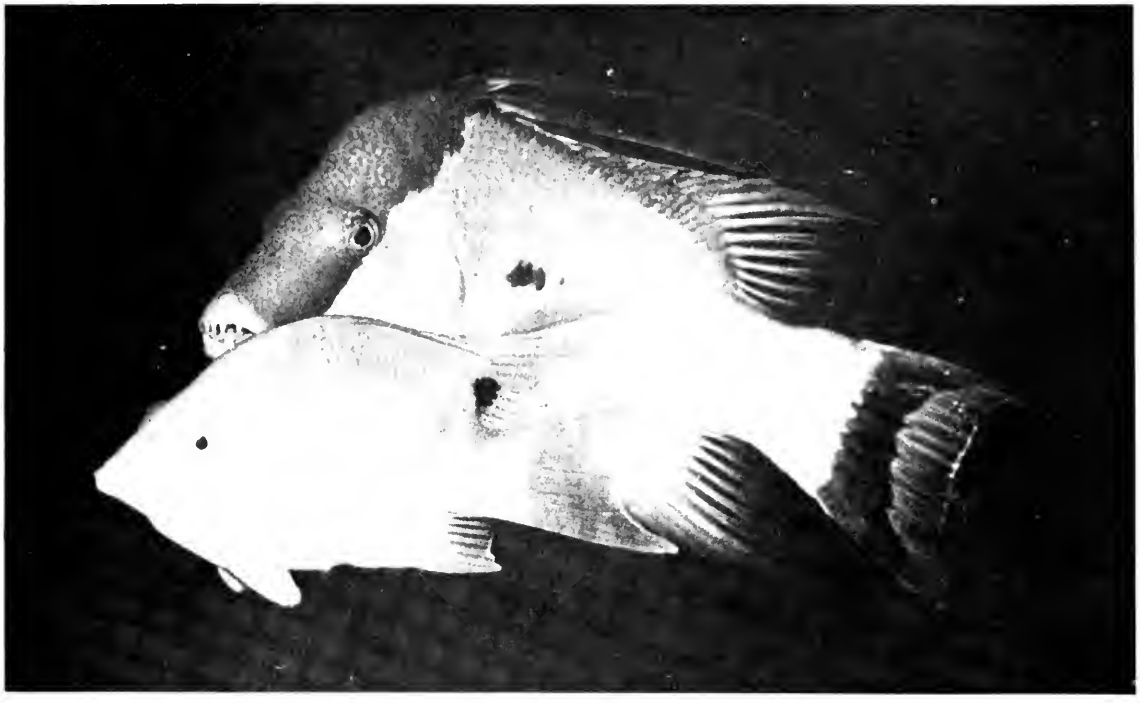

FIGURE 2.—Photograph of spawning pair of *Lachnolaimus maximus* with the smaller female in front of the male. The fish are turning laterally in the "swim alongside and tilt" action just prior to release of the gametes. Photo by C. Arneson at the study site.

to create a turbulent eddy where the gametes had been released to aid in their mixing.

5) Circle and display—When the male broke sharply away from the female, she also turned away, but not as sharply. Both started downward, the male doing a 180° lateral turn while descending. When laterally exposed to the female he initiated a display similar to that used in courtship. The three dorsal spines were erected, the last two shaken. The soft portion of the dorsal and anal fins, the upper and lower margins of the caudal fin, and the pelvic fins were agitated at a rate of 8-10 times/s. This display continued for 1-3 s as the male approached the female and they continued down.

6) Swim down—The male separated from the female and swam downward at a steep angle. She did likewise. He may quickly approach another female and engage in courtship behavior or he may simply rise into the water column if another female is ready to spawn. Occasionally he will court the female he has just spawned with after they have returned to near the substrate, but I have never seen a female spawn two times in rapid succession.

In many instances it was possible to observe the gamete cloud after it had been released. The movements of the fish, particularly the male, produce an area of turbulence where the gametes are thoroughly mixed. On occasion the actual sperm cloud was also faintly visible. Within 15-20 s after release, the gametes will occupy a volume near 1 m^3. There are usually several hundred or more eggs released per rush. In some instances no egg cloud could be found, even though the usual procedures for locating it were followed and the observer arrived within a few seconds to the region in which the eggs should have been. It is possible, but not yet proven, that eggs are simply not released on some rushes.

Yellowtail snappers, *Ocyurus chrysurus*, were active predators on the eggs immediately after release. One to as many as ten yellowtail snappers would converge on the egg cloud 1-2 s after eggs had been released and would pick individual items, presumably eggs, from the water. This occurred in about 20-40% of rushes. Generally if yellowtail snappers observed a pair of *L. maximus* rising to spawn, they would attempt to locate and eat the eggs. On occasion individuals

would follow pairs of *L. maximus* so closely that the spawning rush would be interrupted, causing both the male and female to return to the substrate.

Yellowtail snappers were much more abundant at the actual insular shelf edge than at the hogfish spawning area. At the shelf edge they formed loose aggregations of from several hundred to several thousand individuals feeding on zooplankton high above and beyond the shelf edge. Only a relatively few were found near the moat-moat slope interface, some 100 m away, but these few influenced the reproductive success of *L. maximus*.

Gonad indices of both sexes vary considerably during the year (Davis 1976) in a pattern consistent with my observations. Gonad indices of males for each month ranged from about 0.14 to 0.20 (gonad weight as a percentage of body weight) for December to April and from 0.0 to slightly less than 0.10 for June to August. The indices were relatively low compared with those for other Caribbean labrids (Warner and Robertson 1978) but on a level with those of terminal males (both primary and secondary) of some other species. *Lachnolaimus maximus* is monandric (no primary males) (Davis 1976) and haremic, and the low gonad indices of males are consistent with the data for larger Caribbean labrids of Warner and Robertson (1978). Males are close to an order of magnitude heavier than other "large" Caribbean labrid males (*Halichoeres radiatus* and *Bodianus rufus*) and two orders of magnitude above those of smaller species. Although the gonad indices are low compared with those of other species, the actual gonad is large. The relative size between large and small labrids may not be very important. Males observed in the present study spawned repeatedly each afternoon during the active season. While data for an entire afternoon were not available, I estimated that at least some males engaged in 50-100 spawning rushes/afternoon and that they were capable of fertilizing each group of eggs released.

The female-male ratio among adults also seems higher than in most other Caribbean labrids. Davis (1976) reported a ratio of 13:1 in the 724 individuals he sampled, which is close to the estimated 10:1 ratio that I observed. Warner and Robertson (1978), however, reported a ratio of only 3:1 or less for most species.

The spawning location, about 100 m from the insular shelf edge rather than at the edge itself, appears contrary to some of the concepts put forward by Johannes (1978). It is true that many reef fishes producing planktonic eggs often move considerable distances to be able to release eggs at insular shelf edges where they may be transported offshore. Hogfish, however, rarely move long distances to spawn. Adults can easily range to the shelf edge for spawning and some individuals probably remain along the shelf edge at night after spawning ceases. The potentially heavier egg predation by yellowtail snapper at the shelf edge may help restrict hogfish spawning to more inshore areas. In addition, hogfish are typically found on the sandy margins of reefs where they feed largely on sand-dwelling molluscs (Randall and Warmke 1967) and the moat-moat slope interface area provides both reef shelter and open sand. Territories held by males may also represent feeding areas, whereas the actual shelf edge near the spawning area has little sand, and consists mostly of rock and coral.

EGG AND LARVAL DEVELOPMENT

Eggs are 1.2 mm in diameter and have a single oil globule 0.17 mm in diameter. They float and lack any visible pigment. They hatched 23 h after fertilization at 25.5°C.

Larvae were reared at about 26°C but the temperature could not be closely controlled. When hatched, the larvae had little pigment. Scattered melanophores occurred in the head region and in a line on the dorsal margin of the body (Fig. 3a). They did not orient until about 24 h after hatch, but the eyes were still unpigmented at that stage (Fig. 3b). A line of melanophores along the ventral surface of the body began to develop at this time. Sometime between 24 and 36 h posthatch the eyes became pigmented. First food was added 31 h after hatch. Larvae seemed to be making feeding strikes by about 42 h posthatch (Fig. 3c). At this stage the amount of pigment along the ventral surface of the body increased and was plainly visible to the unaided eye. The black pigment increased daily until 7-8 d posthatch and then remained stable. At 7 d posthatch feeding with *Artemia salina* was initiated. At this time pigment cells were visible on the tip of the lower jaw and on the lower margin of the gill cover. By 10 d posthatch the fin rays had begun to develop, the pelvic fin buds were apparent, and notochord flexion had occurred.

Gas bladder inflation occurred 10 d posthatch (Fig. 3e) in 10-20% of the larvae. Larvae without the bladder inflated would swim with the tail

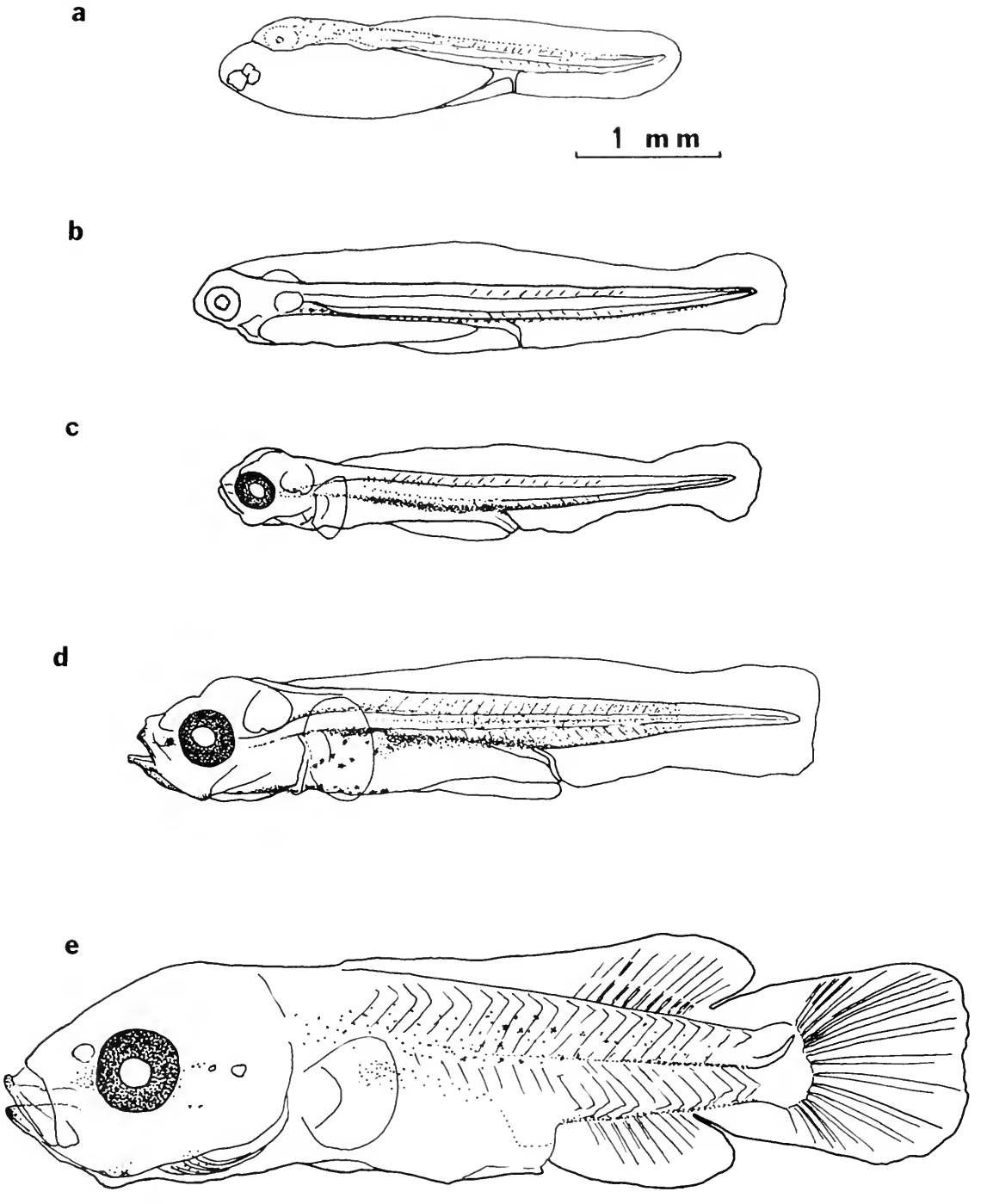

FIGURE 3.—Larval stages of *Lachnolaimus maximus*. a, At hatch; b, 24 h posthatch; c, 42 h posthatch; d, 7 d posthatch; e, 10 d posthatch.

down at an angle of 20°-30° while those with the bladder inflated would swim with the tail slightly up. By 12-13 d the bladders of nearly all larvae had been inflated.

At 13 d posthatch the first traces of the juvenile color pattern began to appear (Fig. 4a) with the development of three pigmented lobes on the base of the anal fin. Widely scattered brown chromatophores appeared on the body, but showed no discernible pattern. At this point the full complement of dorsal, anal, and caudal fin rays had been developed, but the pectoral rays did not seem fully developed. The pelvic fins consisted of only a slight bulge and the first three spines of the dorsal fin were elongated compared with those more posterior. At this stage the fish were considered to be postlarvae.

At 17 d the body had a distinct brown and white color pattern (Fig. 4b) with the first three dorsal spines elongated. At this stage there was little difficulty identifying the postlarvae as *L. maximus*. The postlarvae did not orient to the bottom of the rearing tank, but remained free-swimming. The lights of the rearing tank were extinguished for the first time overnight at 17 d posthatch. Over one-half of the larvae formed

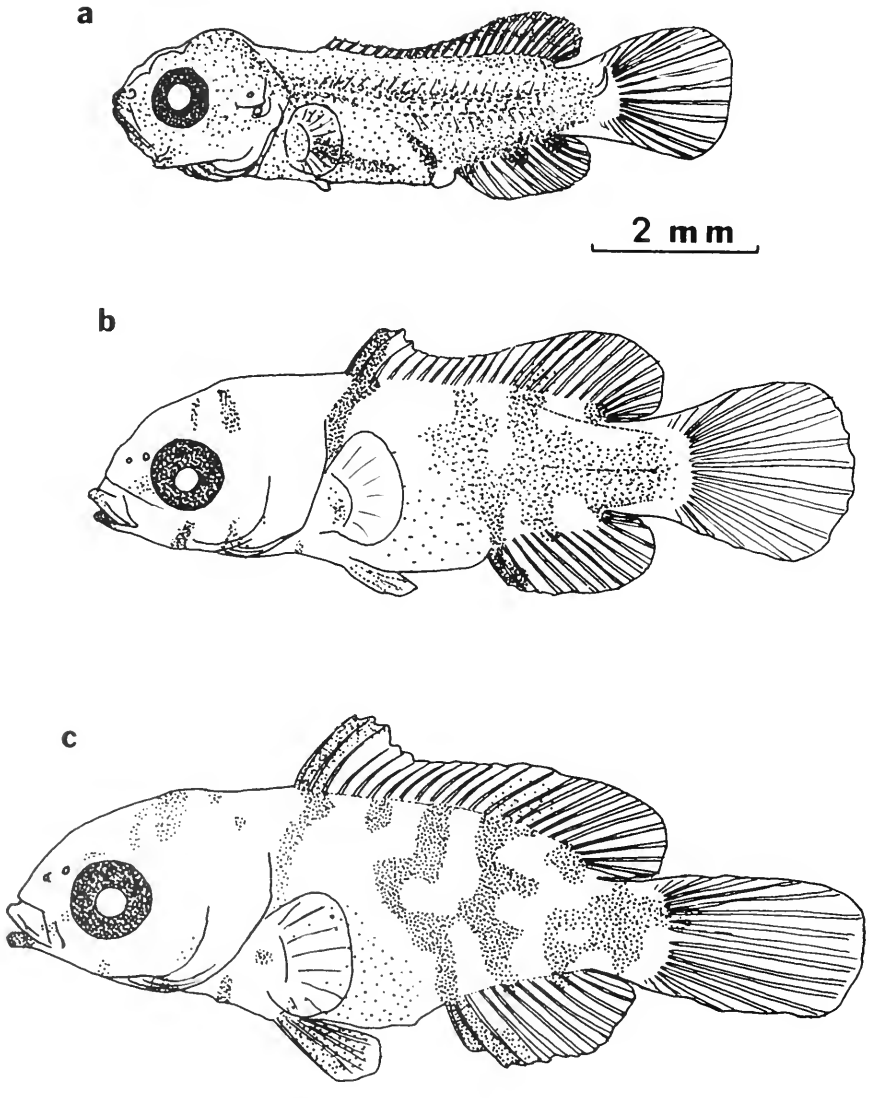

FIGURE 4.—Larval stages of *Lachnolaimus maximus*. a, 13 d posthatch; b, 17 d posthatch; c, 25 d posthatch.

mucous bubbles around themselves that night while floating free in the water near the surface. None rested on the bottom. Such behavior is known in other labrids but had been previously unknown for *L. maximus* or among free-floating individuals. Adults have been observed many times at night with no mucous bubble formation. Bubble formation has not been previously noted for "nonbenthic" labrids. The concept of bubble formation as an antipredator device is supported by its occurrence in postlarvae. Most larvae broke free of the bubbles within seconds after lights were turned on.

At 17 d posthatch, postlarvae tended to stay under material floating on the surface of the water (mostly discarded clumps of mucous bubbles and *Artemia* cysts). Several would stay under a single clump at the surface. No aggressive interactions were noted. Larvae were white and brown, the colors and pattern closely resembling that of *Sargassum*, which may serve as shelter for postlarvae carried into offshore waters.

Ten 18-d posthatch postlarvae were put into an 80 l aquarium with a white sand substrate. Some individuals rested on the bottom the first night, while others remained in the water column, all in mucous bubbles. By 34 d posthatch the fish oriented strongly to the bottom.

Little is known of the early life history of juveniles. Roessler (1964), who reported them from *Thalassia* beds, found some correlation in abundance with density of the bed. The larvae reared in the present study were maintained until about 50 d posthatch, but after about 30 d began dying without obvious cause. They were maintained either in bare aquaria or with a white sand bottom and were never exposed to a *Thalassia* community. They were fed a combination of *Artemia* and wild zooplankton. In their natural environment there may be a diet shift to microinvertebrates at an age when they began dying.

Larvae did not undergo a quick metamorphosis but gradually began to acquire brown and white pigment of juveniles about 13 d posthatch. While still free-swimming the larvae and postlarvae became highly pigmented, which would seem to be a distinct disadvantage in open water. These pigmented young seemed to shelter beneath any floating objects in the rearing aquarium, particularly the shards of their discarded mucous bubbles, which were brown in color. While there are no reports in the literature, their coloration would serve to conceal them in floating *Sargassum* and potentially other floating marine plants. Quick development and the lack of a distinct metamorphosis implies that perhaps the optimum survival strategy to the juvenile stage would be an inshore transport of eggs and larvae and retention of juveniles near the spawning location. Unless associated with floating objects or plants, large *L. maximus* larvae would be at a distinct disadvantage in the pelagic realm. The life history of *L. maximus* implies that the postlarvae become benthic in an inshore location near sea grass beds and subsequently move to offshore reefs (Davis 1976). From the present study there seems no control of spawning condition which would produce an inshore dispersal of eggs (currents, winds, tides, or wave action) and except for seasonal differences, it seems eggs are simply broadcast randomly without the influence of environmental conditions which would influence their ultimate destination.

ACKNOWLEDGMENTS

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BIOLOGY OF THE WHITEBONE PORGY, *CALAMUS LEUCOSTEUS*, IN THE SOUTH ATLANTIC BIGHT[1]

C. WAYNE WALTZ, WILLIAM A. ROUMILLAT, AND CHARLES A. WENNER[2]

ABSTRACT

Whitebone porgy, *Calamus leucosteus*, were taken in trawl surveys over reef and nonreef habitats in the South Atlantic Bight in depths of 11 to 88 m. Larger individuals were taken in greater depths. Twelve age groups can be identified with sectioned otoliths and nine using scales. Annulus formation for otoliths and scales occurs between June and July. Von Bertalanffy growth equations of $L_t = 331\left[1 - e^{-0.1731(t+2.6390)}\right]$ from otoliths and $L_t = 362\left[1 - e^{-0.2611(t+0.3973)}\right]$ from scales suggest that attainment of maximum size for this species is similar to reports for other reef species. The fork length-weight relationship for *C. leucosteus* can be described by $W = 0.00004\ FL^{2.907}$. The whitebone porgy is a protogynous hermaphrodite; younger, smaller fish are predominately females, and older, large fish are mostly males. Sexual transition most commonly occurs between ages II-IV and fork lengths 18-25 cm. Peak spawning occurs in May with total fecundity ranging from 30,400 to 1,587,400 eggs. The fecundity-weight relationship can be described by $F = 10.29438\ W^{1.6562}$. Regional landings data are not available for *C. leucosteus*; however, it was the third and fourth most abundant species by weight from trawler landings in South Carolina during 1979 and 1980.

The whitebone porgy, *Calamus leucosteus*, occurs from the Carolinas south to the Florida keys and throughout the Gulf of Mexico (Fischer 1978). Although more abundant and more frequently encountered in or near sponge-coral habitats at depths from 10 to 100 m (Fischer 1978; Powles and Barans 1980), individuals are sometimes taken from predominantly sandy bottoms (Wenner et al. 1979). This species is of commercial importance to trawl fishermen, but little information is available on its life history. The purpose of this paper is to present data on age, growth, reproductive biology, distribution, and relative abundance of *C. leucosteus* in the South Atlantic Bight.

MATERIALS AND METHODS

Distribution and relative abundance were determined from seasonal (fall 1973 to winter 1977) stratified random otter trawl surveys (Grosslein 1969) from Cape Fear, N.C., to Cape Canaveral, Fla. Sampling was conducted from the RV *Dolphin* with a 3/4 scale version of a Yankee No. 36 otter trawl (Wilk and Silverman 1976) towed for 0.5 h at 6.5 km/h.

Most specimens (~98%) used for analysis of age, growth, and reproductive biology were collected with otter trawls (3/4 Yankee No. 36, 40/54 fly net, University of Rhode Island high rise trawl (Hillier 1974)) from 1975 to 1980. The remainder were caught with baited fish traps and handlines. Fish were weighed (nearest gram) and measured (nearest mm total length [TL], fork length [FL], and standard length [SL]). Sagittae and scales from beneath and/or just behind the posterior edge of the pectoral fin below the lateral line were removed and stored dry. Impressions of several scales from each fish were made on clear acetate sheets with a model C Carver Laboratory Press[3] (1,547-1,687 kg/cm^2, 65.5°C, 5-10 min). Readability was reduced in large otoliths due to clouding of the central area and crowding of the rings along the outer margin; opaqueness also increased in all otoliths with storage time. These problems were corrected by preparing dorsal-ventral cross sections (~0.4 mm thick) on a plane perpendicular to the anterior-posterior axis through the center of the nucleus with a Buehler Isomet low speed saw.

Aging structures were analyzed using transmitted light on a microprojector at 40×. Scale measurements were made on a line through the center of the scale from the focus to the outer edge, whereas otolith measurements were taken from the center of the nucleus to the outer

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

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margin along the ventral edge of the sulcus acousticus. Two independent readings were made on each.

Most analyses were performed using the Statistical Analysis System (Helwig and Council 1979). A FORTRAN program based on Poole (1961) gave back-calculated length at age. The von Bertalanffy growth equation (Bertalanffy 1938) was fitted to mean back-calculated fork length at age using parameters derived from Walford lines obtained by least square linear regressions (Everhart et al. 1975). All regression equations other than the regressions of radial measurement on fork length are the functional regressions of Ricker (1973, 1975).

Sex and reproductive condition of most fish were determined by histological examination of the gonads, which were fixed in formal-alcohol solution (Humason 1972). Tissues were prepared for embedding by passage through an Autotechnicon Duo Model 2A Automatic Tissue Processor. Gonads were embedded in paraffin, sectioned at ~7μ with a rotary microtome, stained with Harris' hematoxylin and counterstained with eosin Y. The first 200 slides were read by two individuals, then, following agreement on interpretation, the remaining sections were viewed by a single observer. Sex and maturity codes were formed by modifying Moe (1969) and Mercer (1978) and applying the four part index of Hilge (1977). The sex codes include hermaphrodite recognition and, when used with the maturity stages, give an accurate and objective estimate of reproductive status. Sexes were identified as undifferentiated, male, female, simultaneous hermaphrodites, male-predominating hermaphrodite, and female-predominating hermaphrodite. Maturity was classed as follows:

Class	*Testicular state*	*Ovarian state*
Immature	little or no spermatocyte development	small, basophilic oocytes
Ripening	from gonads with a few primary and secondary spermatocytes through those where lumen filled with spermatozoa	from relatively acidophilic oocytes through large yolky oocytes
Ripe (running)	predominance of spermatozoa, little active spermatogenesis	predominance of yolk filled oocytes, few hydrated eggs present
Spent	no spermatogenic activity, some residual sperm present in tubules	nonspawned mature eggs becoming atretic
Resting	some mitotic regeneration of spermatogonia	predominately with small basophilic oocytes, few traces of atretic activity
Transitional	resting testicular tissue with ovarian tissue in active development	resting ovarian tissue with testicular tissue in active development.

Terminology used in histological descriptions of gonadal development follows Hyder (1969) and Combs (1969).

Fecundity estimates were obtained from developing ovaries which were weighed (nearest gram) and placed in Gilson's solution (Humason 1972). Following digestion of the connective tissue and external tunic, the eggs were washed and stored in 50% isopropyl alcohol. Eggs were diluted to 1 l, and three to four 1 ml subsamples were removed from a well-mixed suspension, placed in gridded petri dishes, and counted at 12×. The mean of the individual counts expanded to the 1 l volume was used to estimate total fecundity. Histological examination revealed that eggs of diameter <0.15 mm were retained in spent ovaries without signs of atresia, while larger unshed oocytes atrophied. Eggs >0.15 mm were considered potential gametes for the impending spawn and were the only ones included in the fecundity estimates.

RESULTS

Distribution and Abundance

Calamus leucosteus occurred in 94 of 575 stratified random otter trawl tows in depths <110 m during research survey cruises from 1973 to 1977. This species was taken in depths of 11 to 88 m from lat. 28 °50′N to 34°36′N (Fig. 1). Although whitebone porgies were caught over the sandy bottom of the open shelf habitat, they were more frequently taken in trawl tows that contained sponges and corals, indicative of isolated patch reefs. *Calamus leucosteus* was found in 58% of the 67 trawl tows containing live bottom organisms and 11% of the open shelf tows during the surveys from 1973 to 1977. During the spring of 1978, otter trawl sampling in shallow water (18-42 m) sponge-coral habitat from Florida to North Carolina collected *C. leucosteus* in 43 of 57 tows. Thus, *C. leucosteus* may be found in reef and nonreef habitats in the South Atlantic Bight.

Seasonal catch/tow values indicated that *C. leucosteus* moved into warmer offshore waters

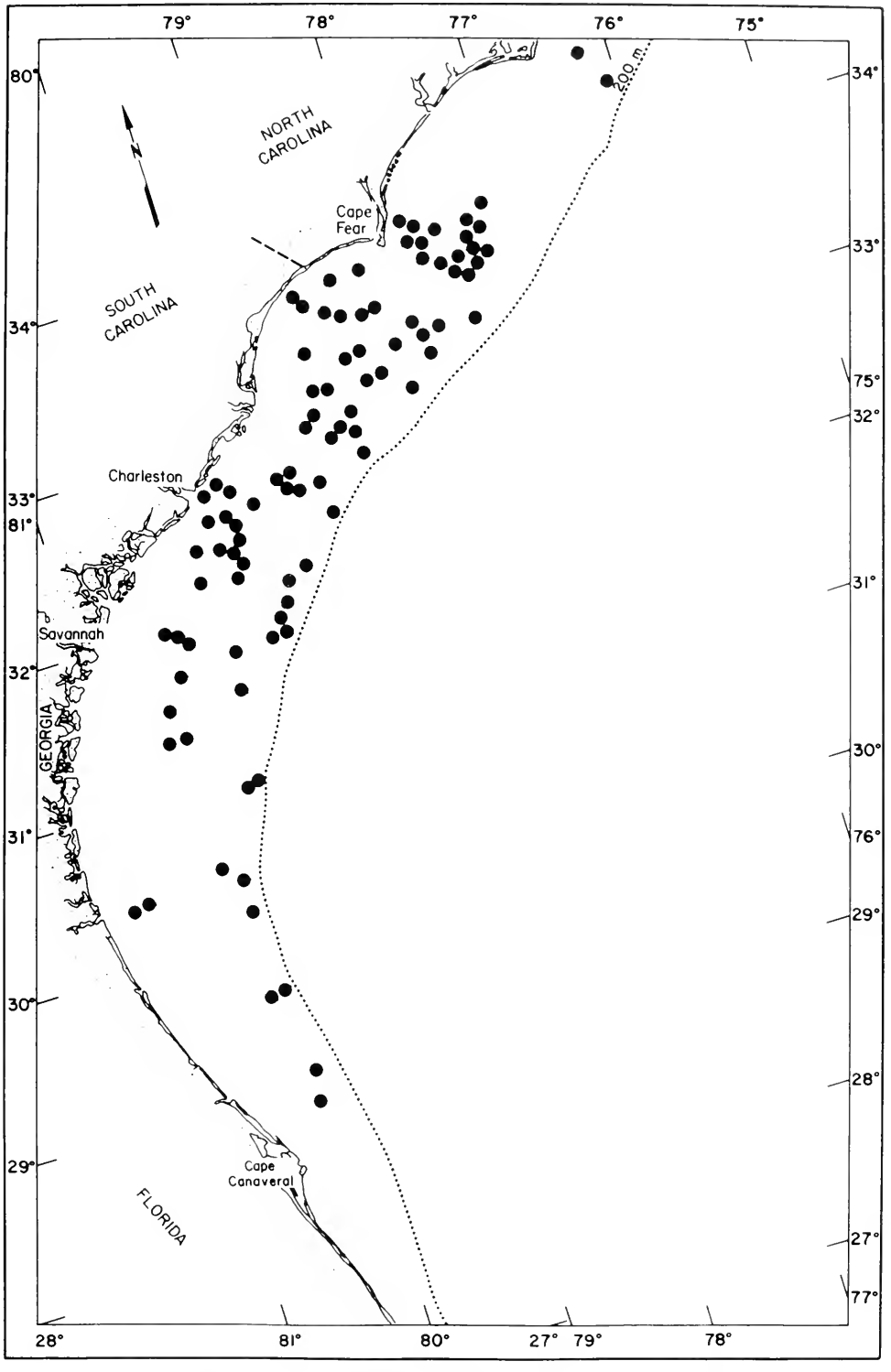

FIGURE 1.—Locations where whitebone porgy, *Calamus leucosteus*, were taken during stratified random trawl surveys from 1973 to 1977.

during winter months, when inshore waters of the South Atlantic Bight have their annual minimum values (Table 1). They were absent in 55 trawl tows made during winter in the 9-18 m depth zone and showed variable frequencies of occurrence in other seasons in comparable depths.

A trend for an increase in modal length with increasing trawl depth was apparent (Fig. 2). All specimens <24 cm FL were encountered in depths <56 m.

TABLE 1.—Catch/tow values from whitebone porgies, *Calamus leucosteus*, from stratified random research surveys from 1973 to 1977. n_1 = number of trawl tows which contained *C. leucosteus*; n = total trawls in depth zone.

Season	Catch/tow	Depth zone (m) 9-18	19-27	28-55	56-110
Winter	$\bar{x}$ catch/tow number	0	4.0	2.0	0.7
	$\bar{x}$ catch/tow weight (kg)	0	1.23	1.07	0.43
	n_1/n	0/55	13/50	9/66	4/42
Spring	$\bar{x}$ catch/tow number	0.3	1.4	0.3	1.3
	$\bar{x}$ catch/tow weight (kg)	0.03	0.55	0.10	1.03
	n_1/n	2/22	5/20	4/28	4/18
Summer	$\bar{x}$ catch/tow number	4 3	2.6	3.1	0.6
	$\bar{x}$ catch/tow weight (kg)	1.12	1.02	1.65	0.43
	n_1/n	9/48	10/50	16/66	5/41
Fall	$\bar{x}$ catch/tow number	2.7	2.6	0.8	0.6
	$\bar{x}$ catch/tow weight (kg)	0.82	1.08	0 24	0.52
	n_1/n	4/18	4/18	3/19	2/14

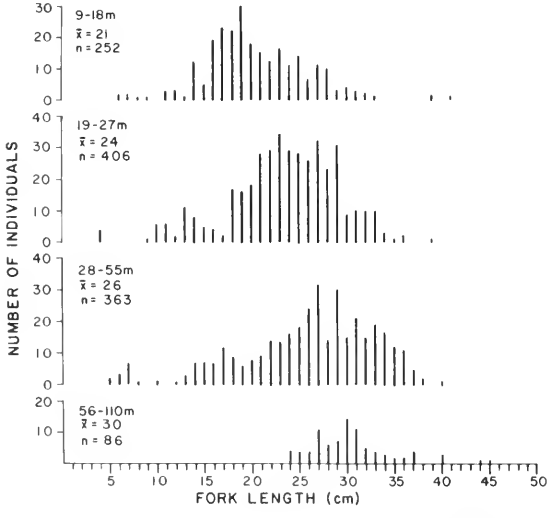

FIGURE 2.—Length-frequency distribution of *Calamus leucosteus* by depth zone for 3/4 Yankee trawl caught specimens (1973-77).

Age and Growth

Life history information was obtained from 1,732 fish collected from 1975 to 1980. Age determinations were attempted for 1,664 pairs of otoliths and 1,679 scale samples, and of these, 80% of the otoliths and 45% of the scales showed discernible rings. There was a 62.8% 1:1 agreement in ages obtained from both scales and otoliths from 760 individuals.

Mean marginal increments by month for scales and otoliths were examined to determine the time of annulus formation (Fig. 3). Samples were combined by month regardless of the year of capture. Mean marginal increments should approach zero at the time of annulus formation; this occurs in June on scales and in July on otoliths.

Fork lengths increased with increasing age as shown by scales and otoliths (Table 2); however, this progression was obscured in older age groups by smaller sample sizes. In general, average fork lengths derived from scale age and otolith age were similar for the first few years, then fish aged by otoliths tended to be smaller then those aged by scales. Fish given identical ages using both scales and otoliths showed average fork lengths at age similar to those derived by scales alone.

The relationships of fork length to otolith and scale radius were best described by the equations

$$\log FL = 1.041 + 0.844 \log OR$$
$$n = 1{,}320 \quad r^2 = 0.70$$

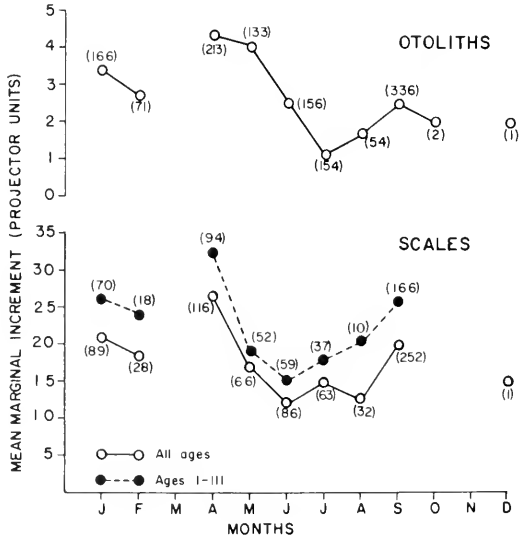

FIGURE 3.—Mean marginal increments for otoliths and scales by month for *Calamus leucosteus*. Number in parentheses = sample size.

TABLE 2.—Mean observed fork length, number and standard deviation (SD) by age for otoliths, scales, and individuals given identical ages by scales and otoliths of *Calamus leucosteus*.

	Otoliths			Scales			Otolith-scales		
Age	No.	$\bar{FL}$	SD	No.	$\bar{FL}$	SD	No.	$\bar{FL}$	SD
0	34	111	22.4	24	98	18.2	16	96	17.9
I	174	153	25.6	122	143	23.4	98	144	22.6
II	319	201	23.5	238	191	22.1	183	194	20.5
III	172	225	23.2	145	225	22.0	93	225	20.1
IV	138	248	22.5	73	256	28.9	41	247	20.0
V	155	263	26.3	77	284	30.8	29	280	27.7
VI	109	280	27.2	54	314	29.0	10	314	19.9
VII	73	284	31.6	18	312	33.5	6	295	44.0
VIII	57	279	32.0	6	345	29.3	—	—	—
IX	34	289	26.1	2	313	66.4	—	—	—
X	25	290	31.5	—	—	—	—	—	—
XI	26	301	33.0	—	—	—	—	—	—
XII	8	309	26.9	—	—	—	—	—	—

$$FL = -36.713 + 1.176\,SR$$
$$n = 757 \quad r^2 = 0.82$$

where FL = fork length (mm), OR = otolith radius (projector units), and SR = scale radius (projector units). The intercepts of these predictive equations were used as correction factors in deriving average back-calculated fork length at age (Table 3). Average back-calculated fork lengths for fish aged with otoliths up to age XII are 136, 179, 207, 227, 242, 252, 259, 264, 273, 280, 291, and 301 mm. For fish aged with scales up to age IX average back-calculated fork lengths were 102, 170, 215, 249, 275, 298, 303, 323, and 306 mm. Average observed fork lengths were greater than average calculated lengths in all cases for otolith and scale ages. Calculated lengths for fish aged with otoliths show a closer agreement with observed lengths than do calculated lengths derived using scales.

Mean back-calculated fork lengths (otolith ages: I-XII; scale ages: I-VIII) were used to obtain von Bertalanffy growth equations. Trial values of $L_\infty = 304$ for otoliths and $L_\infty = 349$ for scales appeared low. We were able to determine the best value of L_∞ by using several trial values of L_∞ and regressing $\ln(L_\infty - L)$ against t, where L = mean back-calculated fork length and t = age (Ricker 1975). The straightness of this line is sensitive to changes in L_∞ and the L_∞ that produced the straightest line was $L_\infty = 331$ for otoliths and $L_\infty = 362$ for scales. Values of $K = 0.1731$, $t_0 = -2.6390$ for otolith ages and $K = 0.2611$, $t_0 = -0.3973$ for scale ages were obtained. The theoretical growth equations derived from these values were

$$\text{otoliths } L_t = 331\left[1 - e^{-0.1731(t+2.6390)}\right]$$
$$\text{scales } L_t = 362\left[1 - e^{-0.2611(t+0.3973)}\right].$$

Theoretical, back-calculated, and observed fork lengths at age for scales and otoliths are compared in Figure 4.

TABLE 3.—Back-calculated fork length at age for *Calamus leucosteus* aged by scales and otoliths.

	Otoliths				Scales			
Age	No.	$\bar{FL}$	SD	Range	No.	$\bar{FL}$	SD	Range
I	1,286	136	17.3	54-231	733	102	20.0	31-183
II	1,112	179	19.3	101-269	611	170	22.9	92-238
III	793	207	21.5	110-273	373	215	26.3	116-297
IV	621	227	23.7	152-303	228	249	28.9	164-334
V	483	242	26.5	165-325	155	275	30.2	189-345
VI	329	252	28.4	180-339	79	298	30.1	200-363
VII	222	259	29.0	186-347	25	303	33.0	238-352
VIII	150	264	28.3	193-360	7	323	42.0	244-366
IX	93	273	28.4	199-354	2	306	63.9	261-351
X	59	280	29.7	209-350	—	—	—	—
XI	34	291	31.3	245-370	—	—	—	—
XII	8	301	24.9	272-340	—	—	—	—

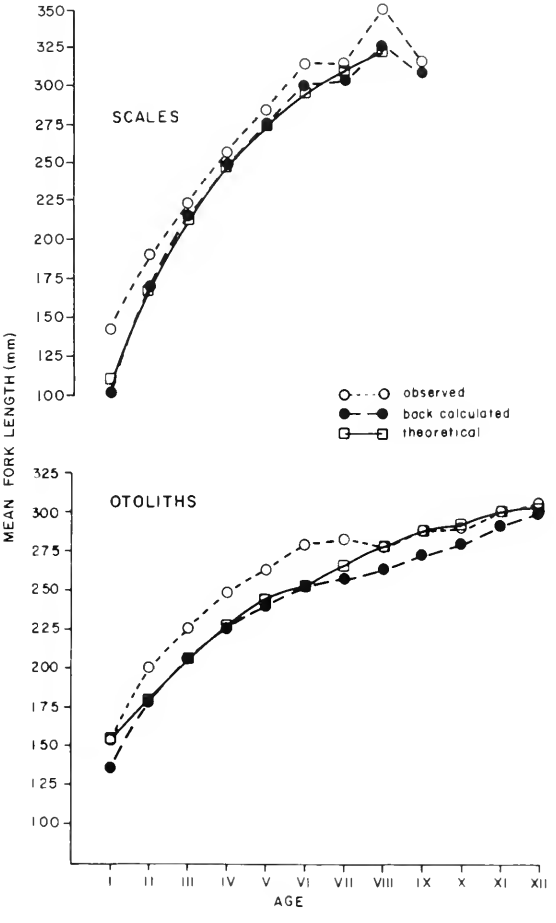

FIGURE 4.—Observed, back-calculated, and theoretical fork lengths of *Calamus leucosteus* aged by scales and otoliths.

Functional length-length and length-weight relationships for *C. leucosteus* are (length in millimeters; weight in grams)

$$FL = 1.13(SL) + 3.9 \quad n = 1464 \quad r^2 = 0.97$$
$$FL = 0.86(TL) - 2.0 \quad n = 1428 \quad r^2 = 0.98$$

$$\log Wt = 2.907(\log FL) - 4.367 \quad n = 1{,}719 \quad r^2 = 0.97$$
$$\log Wt = 2.858(\log SL) - 4.078 \quad n = 1{,}454 \quad r^2 = 0.98$$
$$\log Wt = 2.903(\log TL) - 4.553 \quad n = 1{,}416 \quad r^2 = 0.97.$$

Reproduction

Male and female gonads of *Calamus leucosteus* are paired glands suspended in the posterior body cavity by mesorchia. They join posteriorly into a common duct before the external genital opening. Gonads must be examined histologically for determination of both sex and maturity. Many of the 1,274 fish examined showed protogyny.

Immature female gonads possessed only small (<100 μ), densely basophilic oocytes (Fig. 5A) whereas developing ovaries showed a predominance of larger (~100-500 μ) acidophilic oocytes (Fig. 5B). Paraffin infiltration was poor in large (~500-700 μ), hydrated oocytes and resulted in unsatisfactory sections of ripe ovaries. Atretic oocytes (Fig. 5C) were common in spent gonads whereas resting tissue was identified by traces of atresia and the predominance of small basophilic oocytes. Transitional gonads had most of their bulk as nonactive ovarian tissue, while the testicular tissue was developing (Fig. 5D).

The small, immature testes showed little spermatogenic activity and were largely composed of primary and secondary spermatogonia. Early spermatogenesis and all phases of sperm formation through packing of lumina with spermatozoa (Fig. 6A) were characteristic of developing testes. Ripe testes showed little spermatogenesis with all lumina filled with sperm. Spent testes had convoluted tubules with evidence of residual sperm resorption. The resorptive process was largely completed in resting testes, and mitotic proliferation of spermatogonia had started.

Residual oocytes were present in 58% of the males. These were treated as functional males and all maturity stages (except immature) given to normal males were applied to these primarily male hermaphrodites (Fig. 6B). Traces of nonactive testicular tissue were found in 16.2% of the females (Fig. 6C), and these were treated as functional females. Juvenile hermaphrodites and a few other specimens in which both types of gonadal tissue were not only present, but equally developed, were considered simultaneous hermaphrodites (Fig. 6D). This phenomenon occurred in 3.4% of all gonads and was excluded from further analysis.

Females (Fig. 7) accounted for about 80% of the smaller, younger fishes, while males comprised approximately 70% of the largest size groups and about 80% of the oldest fish. Fish undergoing transition were found in ages I through VII (Fig. 7) and clustered around inflection points of both graphs (lengths: 18-25 cm FL; ages: II-IV). These figures imply that about 20% of young males remain males throughout life and that approximately 20% of the females remain females. Histological evidence demonstrates no case of males transforming to females and indicates females occur in all size and age groups sampled. Thus, approximately 60% of *C. leucosteus* undergo sex reversal.

This species spawns from April to August with peak spawning probably in May (Table 4). Of the fish examined, 100% were developing in March;

TABLE 4.—Percentages of *Calamus leucosteus* in different gonadal states by month of capture.

Month	*n*	Immature	Developing	Ripe	Spent	Resting	Transitional
January	117	2.0	42.4	—	1.0	55.6	—
February	84	—	31.0	—	25.2	41.0	3.6
March	16	—	100.0	—	—	—	—
April	238	11.9	79.1	8.1	1.0	1.0	0.5
May	157	6.4	41.5	32.3	16.0	4.5	—
June	162	17.3	42.1	2.6	14.2	19.8	3.7
July	173	15.6	18.7	3.6	9.9	50.3	—
August	60	1.7	31.7	3.4	1.7	46.7	11.7
September	214	12.7	27.6	—	1.9	44.0	13.6
October	2	—	—	—	—	100.0	—
November	—	—	—	—	—	—	—
December	1	—	—	—	—	100.0	—

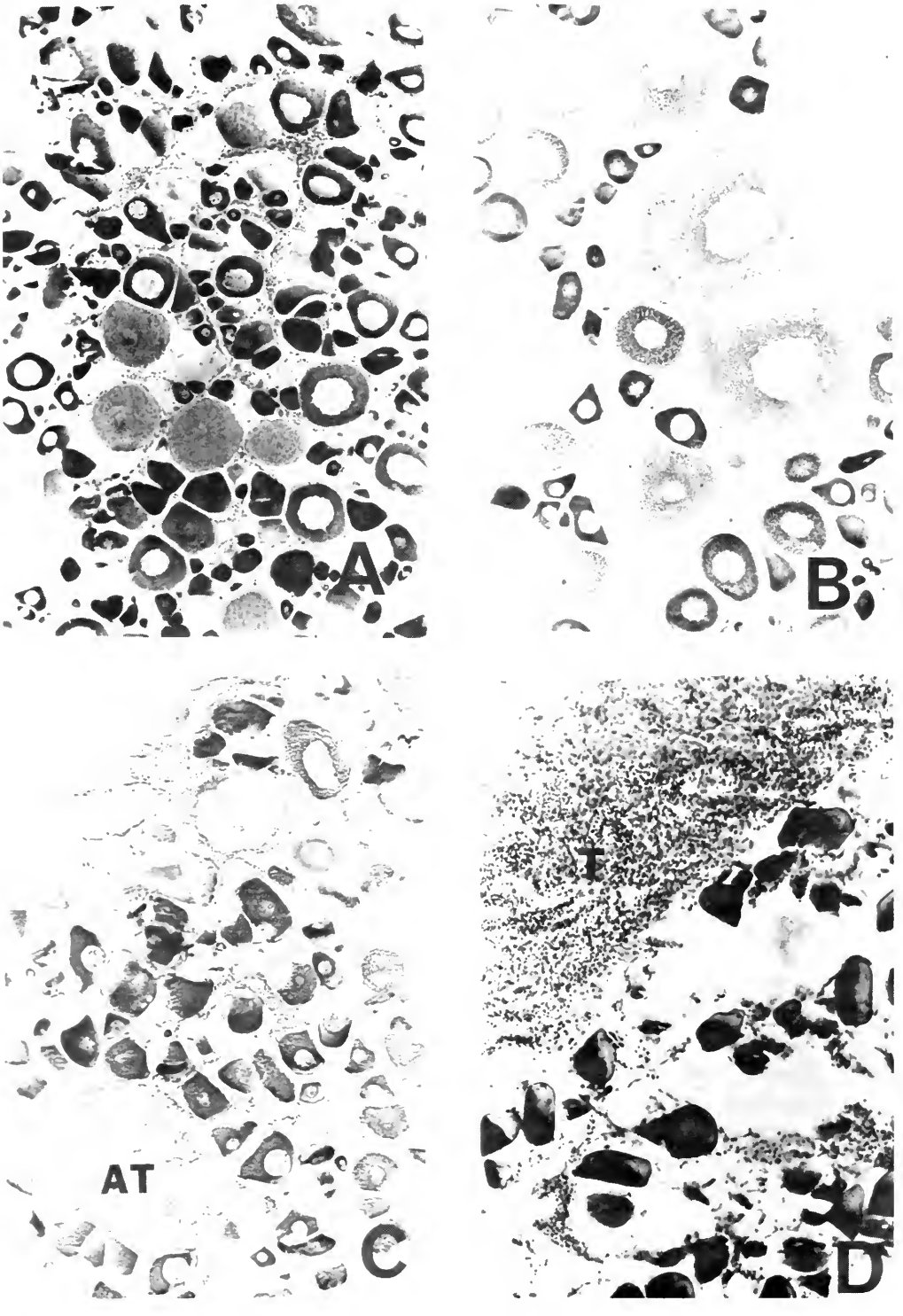

FIGURE 5.—Histological sections of *Calamus leucosteus* gonads. A, immature female; B, developing female; C, spent female; D, transitional gonad. AT = atretic oocyte, T = testicular tissue.

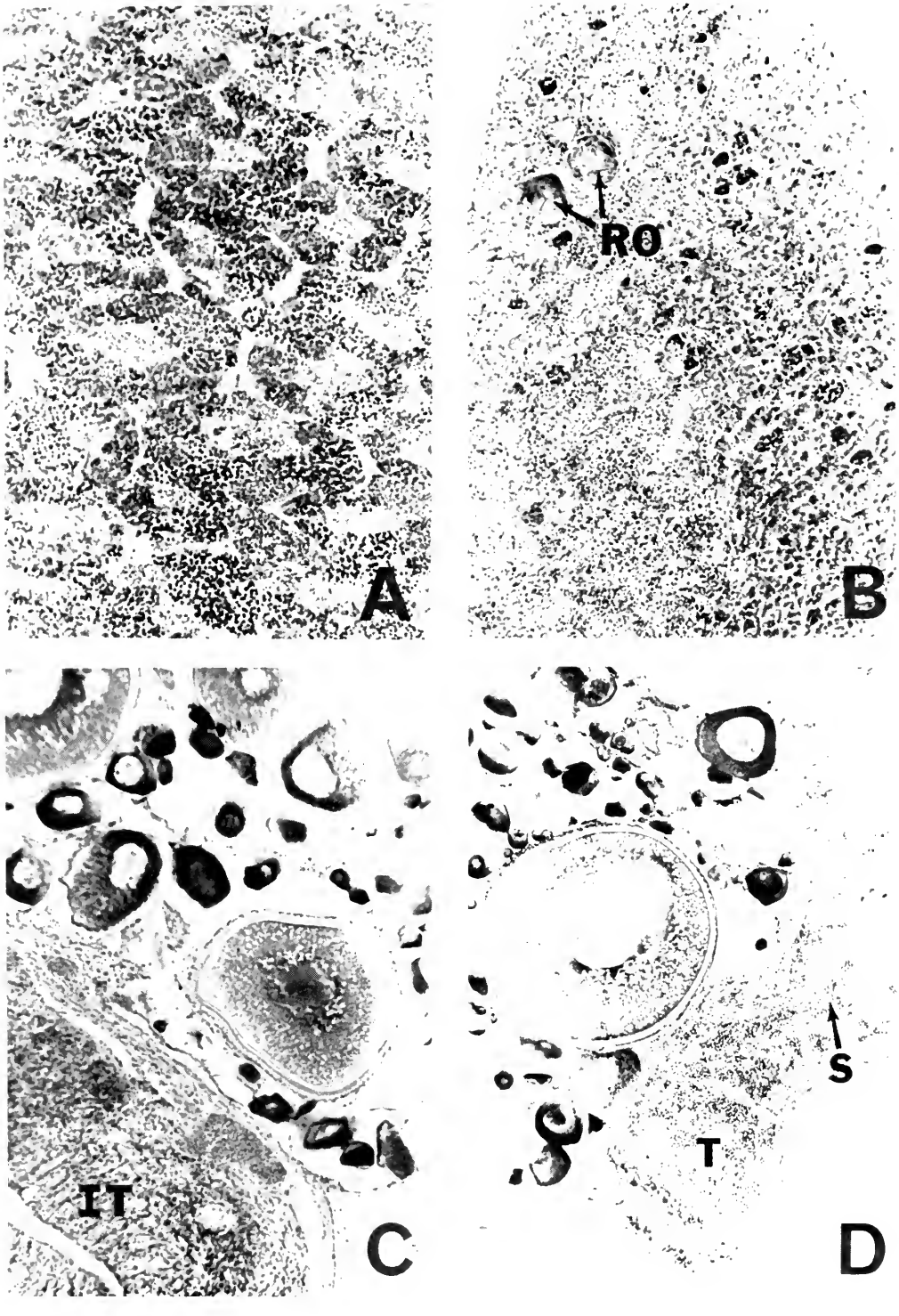

FIGURE 6.—Histological sections of *Calamus leucosteus* gonads. A, developing male; B, developing male with residual oocytes in testes; C, developing female with inactive testicular tissue present; D, simultaneous development in both ovarian and testicular tissue. IT = inactive testicular tissue, RO = residual oocyte, S = spermatozoa, T = testicular tissue.

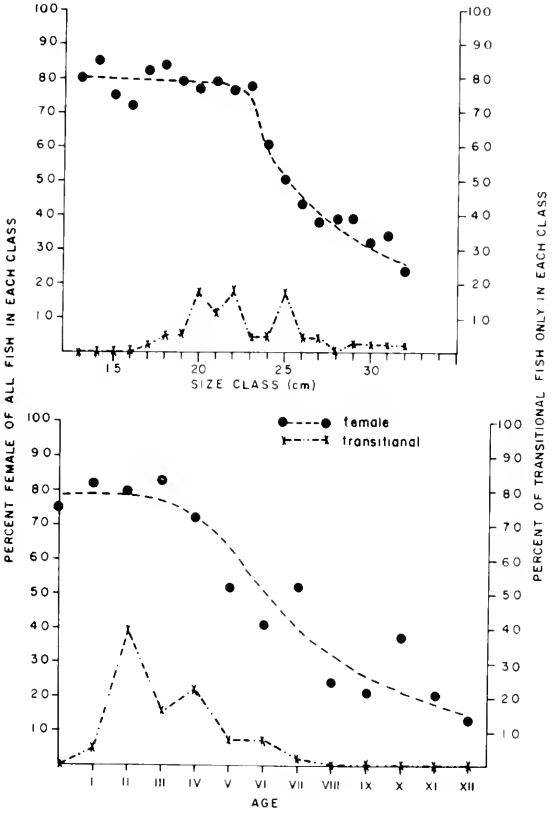

FIGURE 7.—Percent of all *Calamus leucosteus* that were females or functional females and the percent occurrence of transitional fish only by size and age.

this decreased to 79% in April, whereas the highest percentage of ripe fish were observed in May (32%). No ripe fish were encountered before April or after August. Fish undergoing transition were more frequently encountered after spawning (Table 4). The highest percentages of transitional fish were observed in August (11.7%) and September (13.6%). Both sexes may mature at age 1 and females as small as 179 mm FL have been observed with hydrated eggs.

Fecundity ranged from 30,400 to 1,587,400 eggs and generally increased with age (Table 5). It was significantly related to length and weight. The functional regressions for fecundity verses length and weight are

$$\log \text{fecundity} = 4.463(\log FL) - 5.347$$
$$n = 63 \quad r^2 = 0.64$$
$$\log \text{fecundity} = 4.475(\log SL) - 5.093$$
$$n = 63 \quad r^2 = 0.66$$

TABLE 5.—Otolith age-mean fecundity values for *Calamus leucosteus*. The Bliss (1967) approximation was used in transforming the mean from logarithmic to arithmetic units.

Age	Number of individuals	Mean fecundity	Range
I	3	85,192	59,000-129,400
II	11	124,911	30,400-334,700
III	16	215,601	63,700-366,700
IV	5	236,892	119,400-431,400
V	9	285,824	145,000-532,400
VI	4	236,674	60,400-374,700
VII	6	266,348	174,000-617,700
VIII	—	—	—
IX	—	—	—
X	1	869,400	—
XI	1	1,587,400	—

$$\log \text{fecundity} = 4.501(\log TL) - 5.742$$
$$n = 62 \quad r^2 = 0.64$$
$$\log \text{fecundity} = 1.656(\log W) + 1.013$$
$$n = 63 \quad r^2 = 0.66$$

where FL, SL, and TL are in mm and W in g.

South Carolina Commercial Landings

Regional catch and landing data for *C. leucosteus* are available only as the combined values of *C. leucosteus* and *Stenotomus* sp. from the offshore trawl fishery (Table 6). Whitebone porgy represent approximately 98% of these values (Ulrich[4]). The mean size of random subsamples of the trawl catch (1979: $\overline{FL} = 27$ cm; 1980: $\overline{FL} = 26$ cm) was very similar for both years (Fig. 8).

[4]G. Ulrich, Finfish Management Section, Division of Marine Resources, South Carolina Wildlife and Marine Resources Department, P.O. Box 12559, Charleston, SC 29412, pers. commun. 19 May 1980.

TABLE 6.—Reported landings of *Calamus leucosteus* and *Stenotomus* sp. from the South Carolina offshore trawl fishery 1979 and 1980. Values for November and December 1980 are low because of incomplete landings data from one Charleston, S.C. dock.

Month	1979 Weight (kg)	1979 Percent of total catch	1980 Weight (kg)	1980 Percent of total catch
January	1,525	20	4,794	11
February	3,452	18	4,178	9
March	2,722	12	5,081	7
April	2,779	12	3,346	9
May	264	3	560	6
June	132	11	n.a.[1]	—
July	n.a.	—	n.a.	—
August	n.a.	—	n.a.	—
September	n.a.	—	n.a.	—
October	n.a.	—	n.a.	—
November	n.a.	—	2,180	16
December	n.a.	—	1,536	12
Total	10,873	13.4	21,675	9.2

[1]n.a. = not available.

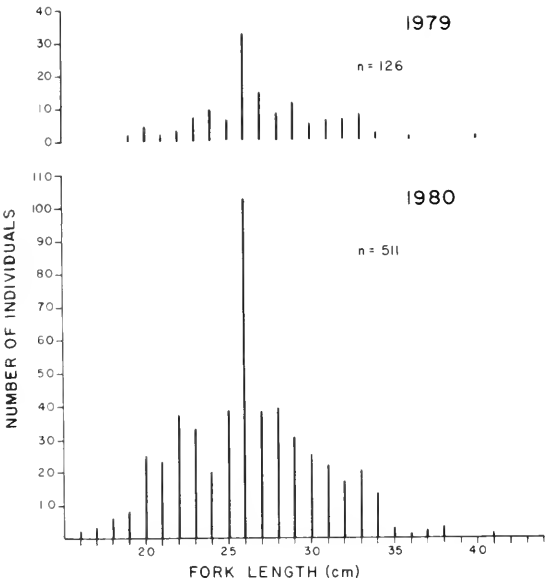

FIGURE 8.—Length-frequency subsamples from trawl caught *Calamus leucosteus* landed in South Carolina offshore trawl fishery, 1979 and 1980.

DISCUSSION

The time of annulus formation is similar in otoliths and scales, it occurs when water temperatures are warm, photoperiod is long, and, in mature fish, just after spawining. The annulus is formed later in the year (June-July) than in some other reef species: vermilion snapper, *Rhomboplites aurorubens*, March-May (Grimes 1978); black sea bass, *Centropristis striata*, March-June (Mercer 1978); red porgy, *Pagrus pagrus*, March-April (Manooch and Huntsman 1977).

Twelve age groups could be identified using otoliths, whereas only nine were determined from scales because of the inability to read those of older fish. In addition, some older fish aged with otoliths had one or more rings than scales. As a result, larger fish aged by scales appear younger than those aged by otoliths, and this is reflected in back-calculated and theoretical lengths at age. The relationship of fork length to otolith radius appears to be curvilinear. The measurement of otolith radius used in this study is actually a measurement of otolith thickness. Beamish (1979) noted in the Pacific hake, *Merluccius productus*, that growth of all parts of the otolith was not identical throughout the life of the fish. He found that growth of older otoliths continues, but that increases in thickness, especially in the ventral interior portion, becomes proportionally more important than increases in otolith length or height. *Calamus leucosteus* appears to be best aged, using this measurement from sectioned otoliths.

Estimates of $L_\infty = 331$ mm FL for otoliths and 362 mm FL for scales appear low since a maximum size of 18 in TL (391 mm FL) was reported by Jordan and Gilbert (1884) and we observed a 407 mm FL fish. The calculation of L_∞ depends on the number of age groups present and the distribution of individuals within each group. Higher values of L_∞ should have been expected if a larger number of bigger older fish could have been aged and included in the calculations. Comparison of growth coefficients (scales: $K = 0.2611$; otoliths: $K = 0.1731$) indicates that *C. leucosteus* attains maximum size at a rate similar to *Centropristis striata*, $K = 0.219$ (Mercer 1978), *Pagrus pagrus*, $K = 0.096$ (Manooch and Huntsman 1977), *Rhomboplites aurorubens*, $K = 0.198$ (Grimes 1978), and red grouper, *Epinephelus morio*, $K = 0.179$ (Moe 1969).

Calamus leucosteus spawns from April through August, with peak spawning in May. Both sexes may mature at age 1 and fecundity estimates range from 30,400 to 1,587,400 eggs. *Pagrus pagrus*, another commercially important sparid occupying the same range, spawns from January through April, matures at age 2, and has fecundity estimates ranging from 48,660 to 488,600 eggs (Manooch 1976).

Calamus leucosteus, as well as several western Atlantic sparids (Reinboth 1970; Manooch 1976; Roumillat pers. obs.), demonstrates protogynous hermaphroditism, which can only be determined by histological observations. Sexual transition in *C. leucosteus* involves the rapid proliferation of testicular tissue in the posteroventral tunica of the ovary which is the typical sparid protogynous pattern (Smith 1975). The testes does not infiltrate the ovarian lamellae as in groupers (Smith 1965), but envelops the regressing female tissue. Male and female tissues are separated during transition by connective tissue, but the sperm ducts pass within the ovarian wall. Other western Atlantic families that demonstrate protogynous hermaphroditism in addition to the Sparidae are the Serranidae (Smith 1965, 1975), the Labridae (Warner and Robertson 1978), and Scaridae (Robertson and Warner 1978). The labrids and scarids have complex socially influenced reproductive strategies that have not

yet been documented for sparids or serranids.

The South Carolina offshore trawl fishery is highly seasonal. Landings are greatest during the winter months after the closing of the shrimp season. *Calamus leucosteus* is the third or fourth most abundant species by weight in trawler landings. These are primarily age IV-VI fish. Red porgy and vermilion snapper are the most abundant trawl-caught commercial fish.

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OBSERVATIONS OF RIGHT WHALES, *EUBALAENA GLACIALIS*, IN CAPE COD WATERS[1]

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ABSTRACT

Sightings of right whales, *Eubalaena glacialis*, in waters within 30 km of Cape Cod, Massachusetts, are reported for 1955-80. Aerial and shipboard observations indicate the occurrence of right whales in this area during most of the year. Sightings peaked during April and May. There were 641 sightings of individual right whales with 117 seen more than 1 day during a year (758 total sightings). Up to 165 whales were seen each year with a maximum 1-day sighting of more than 70 right whales. Behaviors and activities of these inshore whales are described. During the peak period these whales were often found feeding within 5 m of the surface. In other seasons the whales spent less time near the surface and were less visible. These observations do not represent a census because emphasis was placed on the study of the whales found and not on searching to find all the whales in the area.

Observations of northern right whales, *Eubalaena glacialis* Borowski 1781, made in nearshore waters of Cape Cod over a span of 25 yr are reported here, along with characteristic activities, groupings, and differences in visibility of these whales. These sightings (listed in Table 1 and in Schevill et al. 1981) indicated the occurrence of right whales in this area during most of the year and allowed repeated observations of their behavior. Although these sightings were not systematic enough to provide a census of the nearshore whales, they do indicate general patterns that complement more recent efforts to assess the right whale populations and distributions.

Right whales were found in large numbers in the Cape Cod area until about 1730 (Allen 1916), but this stock was systematically reduced by shore whaling that took all that could be caught, including cows and calves. Although heavy harvesting greatly reduced the population, right whales probably have never been totally absent from our waters, even though there seem to have been no published sightings between 1913 and 1955. A review of the historic data was given by Reeves et al. (1978) along with some recent observations.

Since 1955 we have recorded observations of these whales as encountered in Cape Cod waters. Attempts were made to assess their local occurrence, study their behavior, analyze their acoustic activity, and recognize individuals. We have described typical sounds (Schevill et al. 1962; Schevill and Watkins 1962), underwater activity extrapolated from recorded sounds (Watkins and Schevill 1971, 1972), feeding behavior (Watkins and Schevill 1976), and comparison of surface feeding activity with that of three other baleen whale species (Watkins and Schevill 1979).

METHODS

Right whales were observed in Cape Cod waters (Cape Cod Bay, Massachusetts Bay, Nantucket and Vineyard Sounds, Nantucket Shoals, and adjacent waters within about 30 km of the coast, roughly bounded by lat. 41°-43°N and long. 69°-72°W) both from the air and from the water, and occasionally at the same time. The whales were usually within 15 km of the beach, but sometimes were found 30 km or more from shore. Aerial observation allowed assessment of distinctive markings, size (by comparison with the shadow of the fuselage), and activity (feeding, social interaction, etc.). Surface observations from boats drifting quietly alongside the animals permitted photography, underwater sound recording, and behavioral observation. Sometimes contact could be maintained with the same individuals for up to 6 h. Most observations were in daylight, but some nighttime studies were made. In both aerial and shipboard work,

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TABLE 1.—Summary of sightings of northern right whales, *Eubalaena glacialis*, (from Schevill et al. 1981). Repeaters (the same whales seen on more than 1 d during the year) have been subtracted from column D. Searches took place during all months, and there was equivalent search effort during the years 1959-66 and 1972-79. Roman numerals I through XII (Col. A) represent the months January through December.

	A	B	C	D	E	F
Year	Months in which whales were seen	No days whales seen	Total no whales seen	Total no reduced by repeaters	Max. no seen in one group	Max no seen on 1 day
1955	I	1	2	2	2	2
1956	IV	4	24	6	6	6
1957						
1958	IV,V	2	9	9	6	6
1959	III,IV,VIII	16	73	51	7	30
1960	IV,V	6	76	61	16	21
1961	III,IV, V	18	165	131	8	32
1962	I,IV,V	5	15	15	6	6
1963	IV,V	2	5	5	2	4
1964	II,IV,V	8	50	50	4	17
1965	IV,V	6	21	20	3	5
1966	IV,V	5	25	25	4	8
1967						
1968						
1969						
1970	IV	1	70+	70+	30+	70+
1971						
1972	V	2	4	4	2	2
1973	III,IV,V	6	18	18	5	8
1974	IV,V	9	59	58	16	16
1975	I,II,III,IV,V,VI,VII	14	33	28	5	7
1976	III,IV,V,X	8	16	9	2	4
1977	III,IV,VIII,X	10	21	16	7	7
1978	III,IV,VII	10	39	39	9	9
1979	I,III,IV,V,VI	9	20	13	3	4
1980	II,IV,V	7	13	11	4	4
Total		149	758	641		

we customarily remained with the first whales that were found, staying with them as long as they could be studied.

Our searches for right whales were irregular, but were made in all months of the year as weather and other work permitted, mostly under conditions of light wind and good visibility. Fewer trips were made in winter because of poor weather and few sightings, increasing to one to five trips a week in spring with improved weather and greater abundance of whales, and then decreasing during summer and autumn as fewer whales were found. Usually, we made only one trip a day, by aircraft or boat. Sighting efficiency during searches was variable due to changes in weather and whale behavior. From the air, right whales feeding below surface often were located by the light reflected from their baleen. (Though dark above water, baleen appears pale when seen through the sea surface.) Individual whales sometimes were recognizable by natural skin marks and by the pattern of cephalic excrescences (often called callosities) variably covered by light-colored Cyamidae (Leung 1967), a method used for identifying Pacific right whales by Klumov (1962) and southern right whales, *Eubalaena australis*, by Payne (1974, 1976).

RESULTS

In 1955 we identified two right whales from an aerial photograph taken by Bruce M. Clark on 24 January in Cape Cod Bay off Barnstable, Mass. Then in 1956, six whales were found off Martha's Vineyard Island, south of Cape Cod. In 1958 we again found right whales in that area, and in Cape Cod Bay. Active searches began in 1959, and right whale sightings during 21 yr between 1955 and 1980 are summarized in Table 1 and listed in the article by Schevill et al. (1981). No searches were made in 1957 and in 1967-71, although a research cruise through the area in 1970 located a large group of right whales.

The same individual whales were ordinarily sighted for only a few days at a time. Although groups of whales often appeared and then disappeared together, the usual sequence was a procession of right whales through the area. Successive sightings several days apart and within the same area were often of different whales. Right whales were observed alone or in small

groups of two to six adults (49% of the sightings), as cow-calf pairs, occasionally in larger aggregations, and in groups including adults and older calves. A wide variety of sizes was seen, from 5 m calves to adults of from 12 m to about 16 m. Calves were apparently born in these waters, since adults observed without calves sometimes were seen a short time later accompanied by small calves. We found no seasonality or geographic factor that could be related to group size. Sometimes new whales replaced individuals in groups seen on previous days.

During winter and early spring, right whales were difficult to observe because they were at the surface for relatively short periods and were easily disturbed. These whales sometimes blew underwater so that no surface blow (spout) was visible, and they did not always raise their flukes above water as they began a dive. In late spring, the whales were found feeding frequently at or near the surface (Watkins and Schevill 1976), and apparently were less disturbed by our presence. Thus, before the middle of April, sightings were usually short encounters, often sufficient only for identification. Later sightings generally were of more leisurely surfacings, allowing longer periods of observation.

Over the 21 yr there were 641 sightings of individual right whales, with 117 seen on more than 1 d during a year (758 total sightings including repeaters). Some whales were positively recognized as repeaters and others were suspected repeaters because of location, sizes, and markings. During the years 1959-66 and 1972-79, approximately equal time was spent on searches during corresponding seasons in likely sighting areas, although the number of whales and the months and number of days of whale sightings varied markedly (Table 1). The large number seen in 1970 was comprised of at least 30 whales close to our ship (for several hours) and two other large groups of at least 20 each a short distance away, totaling between 70 and 100 right whales. Most of our sightings have been in April (57%) and fewer in May (27%), although we usually have searched more than three times as much in May than in April because of improved weather.

In our usual search, the boat or aircraft first crossed Cape Cod Bay (1-5 times) before rounding Race Point and searching east and north of Cape Cod, and less often south of Martha's Vineyard and Nantucket Islands. Right whales were seen most often near the northern tip of Cape Cod (Race Point) where movement of water masses collects plankton in nearsurface concentrations (Watkins and Schevill 1976). Otherwise, the whales consistently did not seem to prefer locations within the search area. Right whales were sometimes seen a few hundred meters off the beach, but generally they were several kilometers from shore; thus their occurrence cannot be related to bottom topography. No habitual direction of movement was observed.

Few whales were recognized from one year to the next. Callosity patterns provided good separation of individuals within a small group of whales seen in one year, but often have not been distinctive enough for positive identification of animals from the larger population seen over several years. Many of the callosity patterns were similar, and because of the variability in light coloration (apparently caused mostly by movement of the cyamids), fine distinctions in the patterns have been difficult to separate. The callosity pattern on calves appeared to become more visibly distinct with age, perhaps as more cyamids occupied the growths. Comparison of aerial and boat views of the same callosity shapes shows that the nearly vertical aerial view (Fig. 1) loses small details because of distance, distortion through water, and relative density of cyamids, but it provides a good perspective of the pattern; whereas, the nearly horizontal view of the same whales from a boat (Fig. 2) provides good detail, but generally misses the overall shape.

The longest sequence of recognition of an individual right whale was that of a cow seen in 4 consecutive years, 1973-76. During the first and fourth years, this whale was accompanied by a very small calf. In 1974, the yearling calf still accompanied the cow, and in 1975 the cow was in a group that may have included this calf. In 1976, the cow with a new calf was seen repeatedly throughout 7 wk of observation. The pattern of callosities on this cow was very distinctive, but since 1976 a similar pattern has not been recognized.

Groups of right whales generally were involved in social as well as feeding activity. They sometimes broke off from feeding together to chase, splash, and roll against each other, often with three or more whales participating in sexual routines (penises sometimes visible).

The relative ease of sighting right whales depended on their activity at the surface. The respiration period was variable, often averaging 1 blow/min of dive cycle. Dive durations also

FIGURE 1.—Aerial view of two right whales feeding in a slick of collected plankton in Cape Cod Bay, Mass., 1 May 1979 (same individuals shown in Fig. 2). Note the pattern of head callosities and the pale appearance of the baleen underwater. Photo by K. E. Moore.

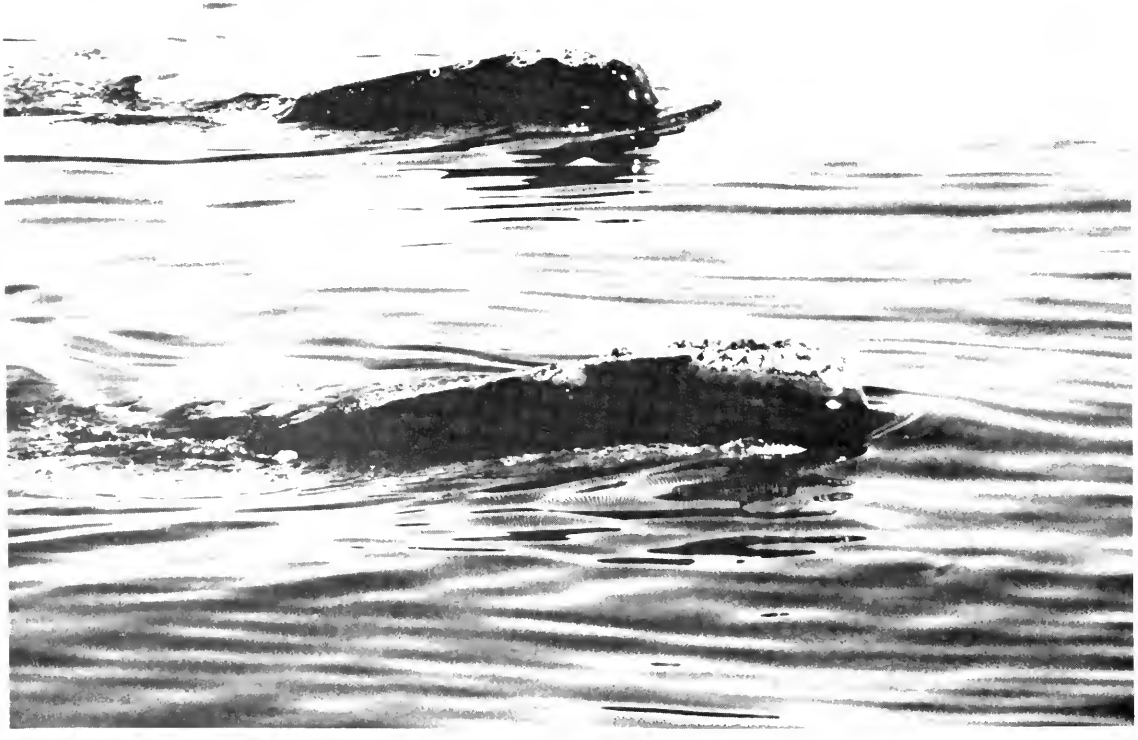

FIGURE 2.—View of two right whales seen from a boat in Cape Cod Bay, Mass., 2 May 1979 (same individuals as in Fig. 1). Note the limitation in visibility through the water surface, yet more visibility in details of head calosity patterns. These whales were observed for nearly 5 h as they fed nearby at the surface, but we found it difficult to record the complete callosity shape from these surface views. Photo by K. E. Moore.

varied from 1 to 7 min during feeding (Watkins and Schevill 1976), with occasional dives of 20 min or longer. Sometimes whales that had been conspicuous in their nearsurface activity suddenly changed their behavior to that of long dives and very little surface exposure.

During two observations of these whales in offshore waters, submergences of 20-22 min with nearsurface times of 10-12 min were recorded, demonstrating less surface activity than in the nearshore sightings. A group of 12 whales was observed at lat. 42°50′N, long. 65°00′W on 9 August 1974 and another group of 7 whales at lat. 42°51′N, long. 65°30′W on 2 August 1976 (not listed in Schevill et al. 1981). Both offshore groups were observed for more than 3 h, but very little surface activity was seen.

DISCUSSION

Our sightings do not provide a basis for a right whale census. Observations were sporadic and directed toward behavioral study, so that we usually remained with the first whales that were found. Although our efforts generally were confined to inshore waters, we note similar patterns reported in offshore surveys (Winn et al.[3]).

Variations in right whale surface behavior probably contribute to variability in sightings. In addition, the elusive behavior often noted in late winter and early spring, coupled with poor weather, may have been responsible for so few sightings during fall and early winter. The peak occurrence (April) of nearshore whales matches Allen's (1916) interpretation of the shore whaling data. He indicated that right whales were most abundant in the nearshore area during April and May, absent in July and August, and apparently abundant from November through March (the period of greatest catch).

The variability in the numbers of right whales sighted in 21 yr, the individual whales' apparent short stay in the area, the changing group compositions, and the few whales recognized from previous years all appear to indicate that we are seeing only a portion of a larger population of right whales. In other places and other seasons, they may not be as visible as they are during their stay in Cape Cod waters.

[3]Winn, H. E., D. R. Goodale, M. A. M. Hyman, R. D. Kenney, C. A. Price, and G. P. Scott. 1981. Right whale sightings and the right whale minimum count. *In* A characterization of marine mammals and turtles in the mid- and north-Atlantic areas of the U.S. Outer Continental Shelf. Annual Report for 1979 Cetacean and Turtle Assessment Program, University of Rhode Island, Kingston, p. 1-37.

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NOTES

FECUNDITY OF THE WIDOW ROCKFISH, *SEBASTES ENTOMELAS*, OFF THE COAST OF OREGON

During the past several years a strong fishery has developed for the widow rockfish, *Sebastes entomelas*. Historical records and the trace amounts captured in early demersal fish surveys (Alverson et al. 1964) contrast sharply with recent catches. Between 1963 and 1977, for example, total catches from 16 to 666 metric tons (t) were landed in Washington, Oregon, and northern California as compared with 19,526 t in 1980 (Demory[1]). Traditional demersal fish surveys have undersampled this species because of both its level of aggregation and its midwater habits (Alverson et al. 1964; Gunderson and Sample 1980) and have therefore not recognized the value of the resource. The increased importance of *S. entomelas* in the west coast trawl fishery has resulted in increased effort to obtain biological information necessary for management of the fishery (Lenarz and Gunderson[2]).

This note is intended to describe the fecundity of *S. entomelas* off Oregon as a function of length and weight, adding to the limited information available from samples collected in 1957 through 1959 and described by Phillips (1964).

Materials and Methods

Sebastes entomelas ovaries were collected in December 1980 and January 1981 during port sampling in Newport, Oreg., by the Oregon Department of Fish and Wildlife. All samples were taken from commercial midwater trawling vessels which had fished off central Oregon (lat. 42°30′ to 45°00′N). While the port sampling was random with respect to size, the samples selected for fecundity analysis were size stratified, and large and small samples were relatively overrepresented. Each specimen was measured to the nearest centimeter in fork length (FL) and weighed to the nearest 10 g; otoliths were removed for subsequent age determination. Ovaries used for fecundity estimates in the present study were those with yolked oocytes corresponding to maturity stage 3 of Barss and Echeverria,[3] although eggs were counted in a few fertilized ovaries which, when collected, showed no signs of extrusion. Whole ovaries were preserved in Gilson's solution modified as described in Gunderson et al. (1980). The solution was changed after approximately 1 wk, and after two more weeks the ovaries were teased apart with forceps and shaken at regular intervals to facilitate separation of ovarian tissue from oocytes. Finally, after approximately 3 mo, the ovaries were put through a coarse strainer under running water, which aided in separating oocytes from ovarian tissue.

Oocyte counts were made by the wet subsampling method (Bagenal and Braum 1968). Oocytes were placed in a beaker and the contents were diluted to a final volume dependent upon the size of the ovary, but varying from 200 to 2,000 ml. The oocytes and water were placed on a magnetic stirrer and stirred until a homogeneous mixture was obtained. Six subsamples (2 ml each) were taken by pipette and placed in vials. Three to six subsamples were counted (depending upon variability of the first three counts) under a binocular microscope. Since all ovaries were mature and within a month of fertilization, there was no difficulty in discerning and counting maturing oocytes. Fecundity was estimated by multiplying the mean number of maturing oocytes per milliliter by the volume of water and oocytes from which the subsamples were drawn.

Results and Discussion

Sixty-eight ovaries from *S. entomelas* were collected, three in December 1980 and 65 in January 1981. Four of the ovaries showed signs of fertilization; although counts were taken on these four specimens, they were not included in the

[1]Robert L. Demory, Oregon Department of Fish and Wildlife, Newport, OR 97365, pers. commun. January 1982.

[2]Lenarz, W. H., and D. R. Gunderson. 1980. Summary of the widow rockfish workshop. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

[3]Barss, W. H., and T. Echeverria. 1980. Maturity of widow rockfish (*Sebastes entomelas*) from the northeastern Pacific, 1977-1981. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

fecundity estimates, which correspond to the "pre-fertilized" fecundity of Raitt and Hall (1967). The distribution of fish lengths for the fecundity samples is shown in Figure 1.

Mean diameter of the preserved, unfertilized oocytes was 0.814 mm and individual means ranged from 0.634 to 0.954 mm. The mean number of oocyte subsamples counted was 4.1 and ranged from 3 to 6. Coefficients of variation of the counts ranged from 0.6 to 10.2% with a mean of 4.6%. As expected, fecundity increased with increasing length, with estimates ranging from 95,375 oocytes at 33 cm FL to 1,113,000 oocytes at 52 cm FL (Fig. 2). Data were fit with linear regressions as used by Gunderson et al. (1980) and with power functions frequently used in fecundity-length relationships (Bagenal and Braum 1968; Raitt and Hall 1967). Although both equations were highly significant, the linear regression provided a slightly better fit to the data but may underestimate fecundity at lengths below about 36 cm FL. Only rarely, however, are females smaller than 35 cm FL sexually mature (Barss and Echeverria footnote 3). A linear relationship was also used to describe the weight-fecundity relationship (Fig. 3). The fitted equations are as follows:

Length

$$F = 59{,}182.4\ L - 1{,}999{,}200 \qquad r^2 = 0.90 \qquad N = 64$$

or

$$\log F = 5.431(\log L) - 3.19 \qquad r^2 = 0.89 \qquad N = 64$$

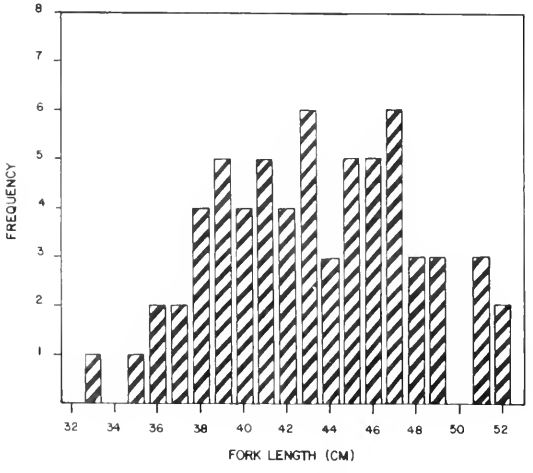

FIGURE 1.—Length-frequency of specimens of *Sebastes entomelas* used in estimating fecundity.

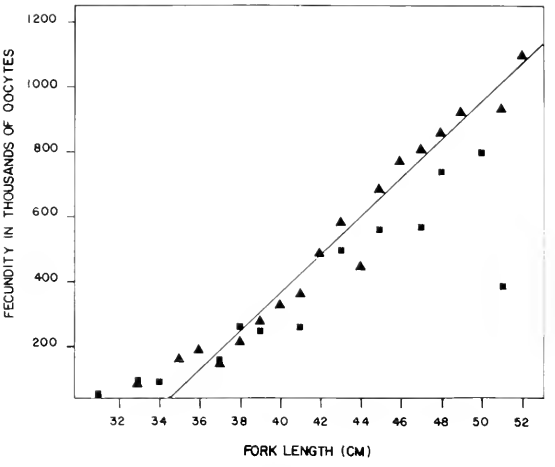

FIGURE 2.—Fecundity of *Sebastes entomelas* as a function of fork length (cm). Triangles represent mean values for fecundity from the present study and the line represents the fitted curve through these points. Squares represent mean values of fecundity from Phillips (1964) with lengths converted to the nearest cm FL. The relationship from the present study is significantly different from that of Phillips (analysis of covariance, $P<0.01$).

Weight

$$F = 605.71\ W - 261{,}830.7 \qquad r^2 = 0.91 \qquad N = 64$$

where F = fecundity (maturing oocytes), L = fork length (cm), W = weight (g), r^2 = coefficient of determination, and N = number of specimens. Fecundity of *S. entomelas* is thus relatively high within the genus *Sebastes*, with values similar to

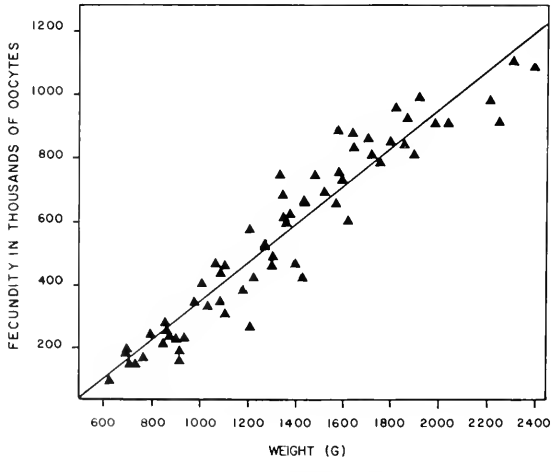

FIGURE 3.—Fecundity of *Sebastes entomelas* as a function of weight. Each point represents an individual specimen.

those of *S. flavidus* and *S. piniger* at equivalent lengths (Gunderson et al. 1980). The mean value of weight-specific fecundity (389 eggs/g body weight) is also relatively high for this genus, as summarized by MacGregor (1970); this value should be considered carefully, however, since weight-specific fecundity is dependent upon size and age (Table 1).

TABLE 1.—Weight-specific fecundity (eggs/g body weight) by age class of *Sebastes entomelas* from the present study. *N* = number of specimens, SE = standard error of the mean. The mean age of specimens >15 yr is 21.5 yr.

Age (yr)	*N*	Specific fecundity (eggs/g)	SE
5	1	151.4	—
6	3	254.0	37.0
7	6	272.9	31.4
8	3	273.3	6.7
9	5	355.3	26.9
10	12	374.7	27.9
11	14	444.9	22.6
12	6	423.4	38.2
13	5	476.8	22.5
14	1	516.1	—
≥15	8	447.4	7.8

The length-fecundity and weight-fecundity relationships described in the present study differ significantly from data presented by Phillips (1964; analysis of covariance, $P<0.01$). The 20 fish in his study were collected from 1957 to 1959 in California. We converted the total length measurements in Phillips to fork length using the total length-fork length relationship in Lenarz[4] and plotted mean values by 1 cm length intervals for comparison with data from the present study (Fig. 2). Values are similar through approximately 40 cm FL, but at greater lengths the values from Phillips are more variable and generally lower than fecundity determined in the present study. Similarly, data on mean weight-specific fecundity was lower; MacGregor (1970) calculated a value of 288 eggs/g from Phillips' (1964) data. As stated above, the mean from the present study was 389 eggs/g. The weight-fecundity regression from Phillips (1964) is characterized by a lower slope. The lines intersect near 1,000 g and Phillips' estimate at 2,000 g is 67.5% of that predicted by the regression from the present study. Gunderson et al. (1980) noted a similar pattern of generally lower fecundity at greater lengths when comparing their data for *S. goodei* and *S. flavidus* with that of Phillips (1964). Since the methods in the present study are most similar to those of Gunderson et al. (1980), methodological differences could explain the different results. Geographic differences, however, may also be involved. Gunderson et al. (1980) noted increased fecundity at length for *S. goodei* in northern as compared with southern geographic regions. Clear differences are also apparent in the length at 50% maturity for several species of *Sebastes*, with maturity occurring earlier in southern areas. Barss and Echeverria (footnote 3), for example, noted that the length and age at 50% maturity for *S. entomelas* females are 38 cm FL and 7 yr off Oregon and 32 cm FL and 5 yr off California. Thus reproductive characteristics within species may differ between areas.

It is probable that *S. entomelas* spawns only once per year. While MacGregor (1970) noted evidence of multiple spawning in three species of *Sebastes*, these species were generally characterized by lower weight-specific fecundity than observed for *S. entomelas*. Furthermore, the lack of a secondary mode of oocytes and the distinct, relatively short spawning season noted by Barss and Echeverria (footnote 3) in both Oregon and California samples indicate a single spawning per year for this species.

Estimates of fecundity from the four samples of *S. entomelas* with fertilized ovaries were below values predicted from the weight-fecundity relationship; the percent of expected fecundity decreased with increasing developmental stage of embryo (Table 2). These specimens had no signs of extrusion of embryos during capture, but it cannot be ruled out. Raitt and Hall (1967), however, noted that egg counts from fertilized

TABLE 2.—Percentage of nonviable eggs and reduction in fecundity in the ovaries of four specimens of fertilized *Sebastes entomelas*. The percent nonviable eggs was determined in four subsamples of 300 eggs. Expected fecundity was determined from the weight-fecundity relationship.

Ovarian stage	% nonviable eggs (±2 SE)	Fecundity (% expected)
Newly fertilized	0.4 (0.17)	87
Late high blastula	1.0 (0.81)	62
Late high blastula	3.2 (0.79)	56
Eyed embryos	0.4 (0.17)	38

[4]Lenarz, W. H. 1980. Aging and growth of widow rockfish. Unpubl. manuscr. Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, CA 94920.

specimens of *S. marinus* were below those of nonfertilized specimens and suggested that the difference was related either to incomplete fertilization or to presence of nonviable eggs which are subsequently resorbed after fertilization. MacGregor (1970) observed undeveloped or unfertilized oocytes from the same batch as developing embryos in all species of *Sebastes* examined, but these accounted for only 0.06% of the egg count in *S. paucispinis*. In *S. entomelas*, this percentage was higher (Table 2). Moreover, since the percentage of expected fecundity decreases with later developmental stage, resorption of nonviable embryos may occur throughout the gestation period. Because estimated and realized fecundity may differ, Gunderson (1977) suggested that fecundity estimates of *S. alutus* be considered tentative. Foucher and Beamish (1980) have made similar suggestions concerning fecundity of the oviparous Pacific hake, noting that nonviable oocytes could contribute to overestimates of fecundity. In the genus *Sebastes* it would thus be interesting to determine fecundity in various stages of developing and fertilized ovaries in a shallow living species which could be captured with no fear of extrusion-related reductions in counts of fertilized eggs or embryos.

Acknowledgments

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A COMPARATIVE STUDY OF AUTOCHTHONOUS BACTERIAL FLORA ON THE GILLS OF THE BLUE CRAB, *CALLINECTES SAPIDUS*, AND ITS ENVIRONMENT[1]

The bacterial flora of blue crabs, *Callinectes sapidus*, has been previously enumerated and identified by examining blue crab hemolymph (Tubiash et al. 1975; Sizemore et al. 1975; Colwell et al. 1975). Other studies on live blue crabs

[1]Contribution No. 82-17C of the Southeast Fisheries Center Charleston Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 12607, Charleston, SC 29412-0607.

have been concerned with the presence of specific human or fishery pathogens in the hemolymph, necrotic tissue, or gill material (Rosen 1967; Williams-Walls 1968; Krantz et al. 1969; Cook and Lofton 1973; Johnson 1976). The statement of Tubiash et al. (1975) that the hemolymph of most healthy blue crabs contains a natural or autochthonous bacterial flora has been challenged, and it has been suggested that further experiments using minimally stressed crabs would be needed to substantiate that statement (Johnson 1976).

This study was designed to determine, seasonally, the natural *Vibrio*, fecal coliform, and aerobic, heterotrophic bacterial populations on blue crabs from environments that differed in salinity and influx of urban and industrial pollutants. These microbial populations were also compared with those found in intertidal oysters (*Crassostrea virginica*), waters, and sediments collected simultaneously with the crabs. Blue crab gills were chosen as a suitable substrate for microbiological investigations because they have direct contact with the environment and are easily sampled and processed for enumeration of their bacterial flora.

Materials and Methods

Two South Carolina areas, Charleston harbor and St. Helena Sound, an estuary 35 mi south of Charleston, were surveyed during a 22-mo period between August 1979 and May 1981 (Fig. 1). Within each area, two sampling stations were selected, representing mean salinities of 10‰ and 25‰. The Charleston harbor sampling stations were Foster Creek, salinity 10‰, a tributary to the Wando River, which, along with the Ashley and Cooper Rivers, forms Charleston harbor; and Shutes Folly Island, salinity 25‰, situated near the center of Charleston harbor. The oyster beds in both sites are closed to harvesting because fecal coliform levels, monitored in the water column and oyster meats by the South Carolina Department of Health and Environmental Control, exceed safe limits for harvesting areas. Foster Creek receives negligible industrial pollution, whereas the Shutes Folly Island station receives a moderate-to-heavy influx of industrial pollutants. The St. Helena Sound stations were the Ashepoo River at Mosquito Creek, salinity 10‰, and St. Helena Sound at the mouth of Rock Creek, salinity 25‰. Shellfish beds at these stations are open to harvesting, with no discernible influx of urban, industrial, or commercial pollutants. Each station was sampled on a quarterly basis to coincide with the highest and lowest temperatures in the water column and during the middle of the two transitional periods in water temperatures.

Blue crabs were captured in commercial-type crab pots baited with fresh fish heads. The crab pots were harvested from 4 to 24 h after being set, dependent on the seasonal rate of blue crab capture. Intertidal oysters and sediments from the oyster beds were collected manually at low tide. Two hundred grams of the top centimeter of sediment were removed with sterile tongue depressors and placed in sterile containers. Surface water samples (1 m below the surface) were collected with a Niskin[2] sterile bag sampler (General Oceanics, Miami, Fla.) at the site of blue crab collections. All sediment, water, and oyster samples were immediately cooled with ice. Blue crabs were maintained at their in situ temperature by placing them in a thermally insulated container. All samples were analyzed within 4 to 8 h. During a survey, two to four representative composite samples of blue crab gills (dependent on seasonal activity of blue crabs), three oyster composites, and two samples each of sediment and surface water were collected and analyzed for each sampling station. A composite gill sample contained gills from 10 to 12 crabs. Since mature female blue crabs migrate to higher salinities, male blue crabs dominated the population at 10‰ salinity and females at 25‰ salinity. Whenever possible, blue crabs above the legal harvesting size for South Carolina, 127 mm, were sampled. Each survey was completed within 4 d. For monitoring purposes, temperature and salinity of the surface water were measured, using a YSI Model 33 Salinity-Conductivity-Temperature meter (Yellow Springs Instrument Co., Yellow Springs, Ohio).

Preparation of oyster and water samples for analyses followed standard procedures (American Public Health Association 1970, 1976). Carapaces of the blue crabs were cracked vertically with a blow from a stainless steel knife. The knife did not penetrate into the gut or organs. The carapace was then removed by pulling up on the lateral spines (Fig. 2). Exposed gills were aseptically removed with forceps and placed in

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

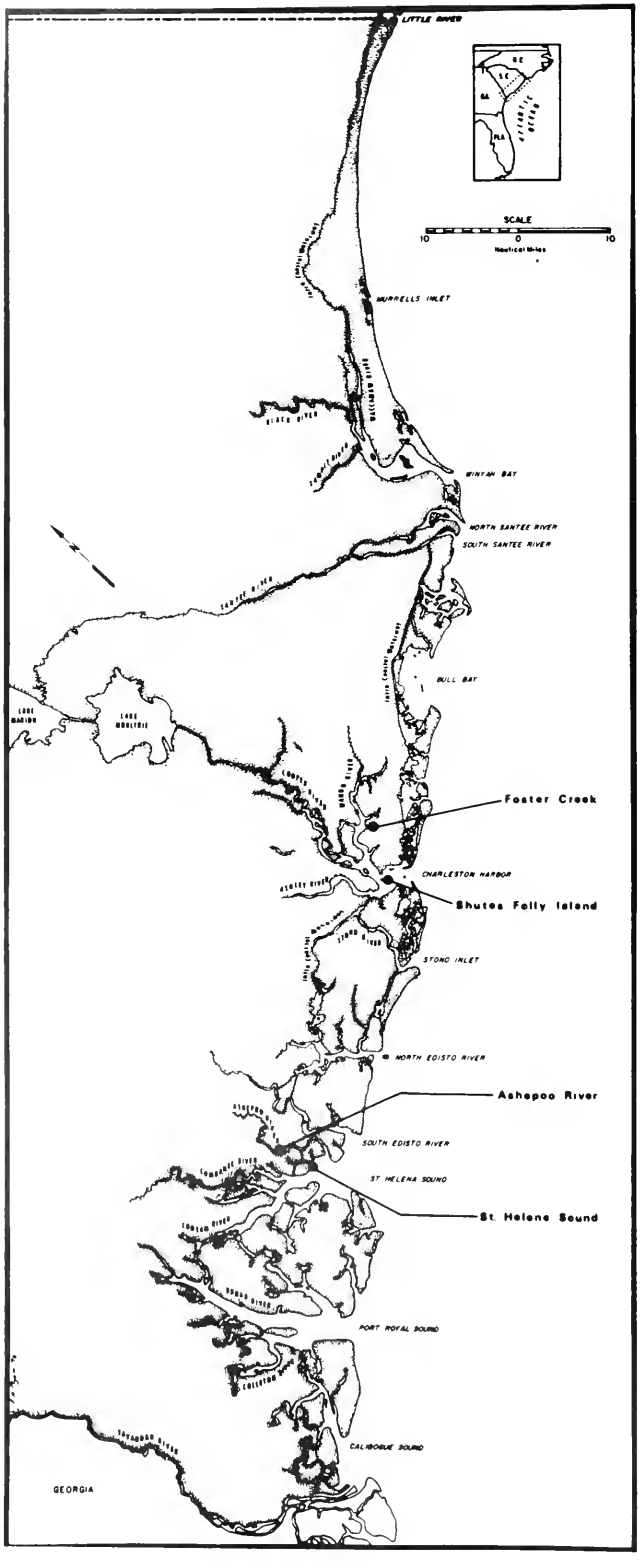

FIGURE 1.—Map of coastal South Carolina showing location of sampling stations.

FIGURE 2.—Photograph of blue crab with section removed from vertically cracked carapace.

sterile containers. The blue crab gills were homogenized in a blender for 2 min at high speed and further prepared for bacterial analysis following the standard procedure for oysters. Blue crab gills and oysters were analyzed on a wet-weight basis (50 g), but sediments were analyzed on a volume-to-volume basis (50 ml) because of the great differences in sediment densities found in the environment. The initial dilution was made by volume displacement of the diluent by the sediment in a calibrated container as previously described (Babinchak et al. 1977). All dilutions were made using sterile 0.1% peptone (Difco Laboratories, Detroit, Mich.) saline solution (1.5% NaCl).

Total viable, aerobic, heterotrophic bacterial counts for all samples were determined, using the spread-plate technique and a modification of a low-nutrient, artificial seawater plating medium (ASWLN) of Litchfield et al. (1975) containing the following ingredients per liter of half-strength artificial seawater (Rila Marine Mix, Teaneck, N.J.): 0.5 g peptone (Difco), 0.5 g yeast extract (BBL Microbiology Systems, Cockeysville, Md.), 0.1 g sodium glycerophosphate (MCB Manufacturing Chemist, Inc., Cincinnati, Ohio), and 20 g agar (BBL). Three replicates of each dilution were plated, and the inoculated plates incubated at 20°C for 14 d.

Fecal coliform counts in all samples were estimated by the three-tube most-probable-number (MPN) procedure prescribed for seawater and tissues (American Public Health Association 1970, 1976). Lauryl sulfate tryptose broth (BBL) was used in the presumptive test, with confirmation in EC broth (BBL) incubated at 44.5°C in a circulating water bath.

Vibrio-like organisms were enumerated on thiosulfate citrate bile salts agar (TCBS; BBL) using the spread-plate technique for all samples. Fifteen to thirty colonies, representing all colonial types, as determined with oblique or darkfield illumination through a stereomicroscope, were picked only from the blue crab gill-inoculated TCBS plates. The cultures were purified and then characterized biochemically using the API 20E system (Analytab Products, Inc., Plainview, N.Y.).

Results

During the initial survey, it was noted that many intermolt blue crabs had dark brown or mahogany-colored gills which contrasted with the light-colored gills of recently molted crabs. The light- and dark-colored gill material was subsequently divided and analyzed separately.

The microbiological data from 61 blue crab gill samples collected during five quarterly surveys were analyzed statistically using a generalized analysis of variance (ANOVA) employing the maximum likelihood approach. The dependent variables for analysis were the microbial counts on the blue crab gills; independent variables were urban and industrial pollution, salinity, season, gill color, and their pairwise interactions. In Table 1, the *P*-values resulting from the analysis of variance indicated that season, gill color, and the interaction of pollution and season affected the total *Vibrio* and aerobic, heterotrophic bacterial counts. Fecal coliform counts were not significantly affected by any of the variables investigated.

Graphically displayed in Figure 3 is the effect of season and gill color on total *Vibrio* and aerobic, heterotrophic bacterial counts. Dark gills had consistently higher counts, and the counts showed a similar pattern with season.

Surprisingly, the absence of urban fecal pollution had no significant impact on fecal coliform counts in blue crab gills (Table 1). Blue crab gills obtained from St. Helena Sound, a pristine area, yielded high fecal coliform counts, whereas intertidal oysters and waters sampled concurrently were relatively free of contamination (Table 2). To confirm the identity of the fecal coliforms found in St. Helena Sound, 90 bacteria were isolated from positive EC broth MPN tubes, checked for their Gram reaction, and analyzed biochemically with the four reactions which constitute the IMViC differential test (American Public Health Association 1976). The sources for the bacterial isolates were blue crab gills (35), water (26), sediment (15), and oysters (14). Ninety-four percent of the isolates were identified as typical *Escherichia coli* and 6% as typical *Enterobacter aerogenes*. Twenty fecal coliforms isolated from blue crab gills were also tested with the API 20E system, and all identified as *E. coli*. Representative samples of blue crab stomach contents analyzed in parallel with the

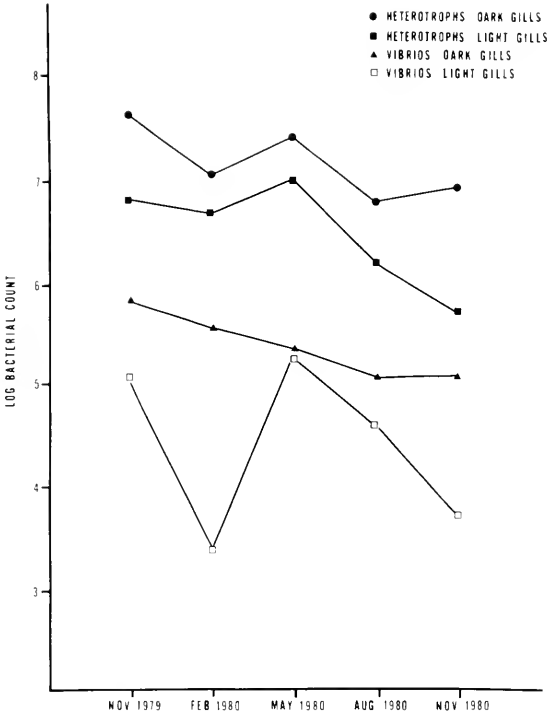

FIGURE 3.—Average total *Vibrio* and heterotrophic bacterial counts per gram of light and dark crab gill tissue from all samples collected from the St. Helena Sound area.

TABLE 1.—*P* values resulting from generalized ANOVA of crab gill data. The hypothesis that a factor has an effect on microbial counts in blue crab gills is accepted when $P \leq 0.05$.

Independent variables	*P*-values, dependent variables		
	Heterotrophs	*Vibrio*	Fecal coliforms
Pollution	0.748	0.233	0.304
Salinity	0.549	0.207	0.211
Season	0.030	0.015	0.355
Gill color	0.001	0.001	0.312
Pollution - salinity	0.916	1	1
Pollution - season	0.001	0.036	1
Pollution - gill color	1	1	1
Salinity - season	1	1	1
Salinity - gill color	1	1	1
Season - gill color	1	1	1

TABLE 2.—Distribution of fecal coliforms in samples collected from St. Helena Sound area.

Sample	Fecal coliforms/100 g[1]				
	Nov. 1979	Feb. 1980	May 1980	Aug 1980	Nov. 1980
Intertidal oysters	21	12	12	21	160
Water	80	5	2	16	12
Sediment	430	340	60	19	90
Blue crab gills	2,000	4,300	230	4,300	210

[1]100 ml of water and sediment samples.

corresponding gill tissues gave significantly lower heterotrophic counts.

Dark blue crab gills harbored the same heterotrophic bacterial populations found in the sediments (Fig. 4). Similar results with total *Vibrio* populations were obtained in these areas. As shown in Figure 4, oysters and water contained lower heterotrophic counts.

Only 10 to 30% of the TCBS bacterial isolates from individual samples of light and dark gills could be identified to genus and species using the API identification system. *Aeromonas* spp. made up 28% of those TCBS isolates identifed.

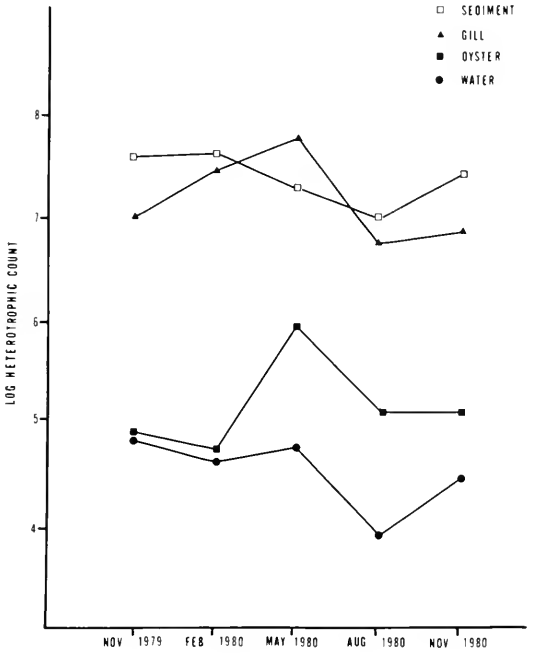

FIGURE 4.—Average heterotrophic bacterial counts per gram of sample collected quarterly from Foster Creek.

Discussion

Common external features which distinguish blue crabs with brown to mahogany gills are rust-spotted exoskeletons and, occasionally, attached barnacles and algae. These conditions are not considered abnormal for late intermolt crabs. Johnson (1977) has also described a viral disease in which blue crabs displayed similar diagnostic signs: failure to molt, a brown-spotted exoskeleton, and gills that were often red-brown.

Sections made from dark gills collected during the survey showed that these gills were, to varying degrees, fouled by a layer of bacteria and mucus (P. T. Johnson[3]). Observations of similarly fouled gills of rock crabs, using scanning electron microscopy, showed large numbers of bacteria residing on the gill tissue, similar to those found on blue crab gills in this study using bacterial enumeration procedures (F. Thurberg[4]).

These enumeration data suggest that the gills of blue crabs provide an ecological niche for the growth and physiological activity of heterotrophs, *Vibrio* spp., and related organisms, equivalent to that described for sediments and zooplankton (Kaneko and Colwell 1975 a, b, 1978). The high fecal coliform population found in our pristine area would indicate that gill surfaces also provide a protective ecological niche much like that reported for marine sediments, where high fecal coliform populations can accumulate and persist even in ecosystems where influx of fecal coliforms is low (Rittenburg et al. 1958; Van Donsel and Geldreich 1971; Babinchak et al. 1977).

Urban and industrial pollution did not have an effect on total *Vibrio* and aerobic, heterotrophic bacterial counts on blue crab gills. Since these two microbial populations are indigenous and dependent on nutrient levels for growth, industrial and domestic pollution would not necessarily have shown an effect over the pristine areas sampled. The vast marshlands which drain into the St. Helena Sound area (Tiner 1977) would introduce large natural levels of dissolved and particulate organic material and other nutrients which could support the high bacterial levels observed.

The low rates of identification by the API 20E system can be attributed primarily to the high percentage of clinical bacterial isolates which form the API data base. Even some of our positive identifications are now in question, because marine isolates identified as *Aeromonas* spp. with the API system are known to be Group F vibrios (Seidler et al. 1980). This group of *Vibrio*-like organisms has been associated with diarrheal illness, although the epidemiology of the disease has not been well-defined.

[3]P. T. Johnson, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Oxford, MD 21654, pers. commun. 1981.

[4]F. Thurberg, Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Milford, CT 06460, pers. commun. 1981.

The data obtained in this study establish blue crab gills as excellent surfaces for enumerating the blue crab's natural adherent bacterial population. Bacterial quantitation, which is difficult to achieve with other crab surfaces, is easily accomplished with gills. Succession of bacterial species and the possible influence of environmental contaminants in the bacterial colonization of blue crab gills are also conveniently accommodated by the molting process. The freshly molted gill surfaces can be compared with gills that have been exposed to the environment for extended periods. Gill surfaces may provide a model system for monitoring biological or chemical pollutants based on observable changes in the autochthonous bacterial populations of blue crab gills.

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WHITE SHARK PREDATION ON PINNIPEDS IN CALIFORNIA COASTAL WATERS

White sharks, *Carcharodon carcharias*, prey on various fishes, sea turtles, whales, dolphins, and on several species of pinnipeds (Allen 1880; Elliot 1881; McCormick and Allen 1963; Davies 1964; Nishiwaki 1972; Ellis 1976; Ainley et al. 1981; McCosker 1981). Data on pinnipeds preyed upon by sharks in California waters are meager and many aspects of the predator-prey relationship are unknown.

Four types of evidence indicate that sharks prey on pinnipeds: 1) Pinniped remains in the stomachs of dead sharks, 2) observation of seals with injuries inflicted by large sharks, 3) observation of shark attacks on seals, and 4) the presence of sharks near seal rookeries at a time when seals are present. We report evidence of the first two kinds regarding shark predation on northern elephant seals, *Mirounga angustirostris*, and harbor seals, *Phoca vitulina*.

Methods

Five white sharks caught in southern California waters in 1975 and 1976 and two white sharks that washed ashore in central California in 1977 and 1978 were examined. The fresh dead sharks were weighed, measured, and their sex determined. Stomachs were dissected out and contents identified, and in some cases, weighed and measured (Table 1).

From 1968 to 1980, shark-bitten elephant seals on Año Nuevo Island and the adjacent Año Nuevo Mainland in central California were counted, photographed, and identified individually, and their behavior was monitored. This was accomplished during daily censuses conducted each breeding season from December to mid-March and during weekly censuses conducted during the remainder of the year. Only seals with fresh wounds judged by their pink or bloody appearance to be less than a few days old were included in the sample. This gives us confidence that our subjects were injured near the study area. We did not census animals with old scars or healed injuries, whose origins were difficult to ascertain. Shark injuries were differentiated from other wounds, caused by boat propellers or intraspecific fighting, by their oval shape and the jagged serrations caused by the predator's sharp teeth. Both slight and serious wounds were included. Slight wounds consisted of superficial tooth punctures or scrapes across the skin; serious wounds involved deep bites and tears. Seriously wounded seals had large flaps of flesh exposed or chunks of flesh missing. The dimension of bites was measured on a few dead seals.

We marked and followed 11 females who sustained moderate to severe shark wounds when pregnant just before arriving on the island to give birth. Their pups were marked at birth and the pair was observed until the filial relationship ended. Northern elephant seal females give birth within a week after arriving on the rookery. A female nurses her pup daily for about 4 wk before weaning it and returning to sea (Le Boeuf et al. 1972).

A similar search for shark-bitten harbor seals, which breed at Año Nuevo Island and numerous

TABLE 1.—Stomach contents of white sharks collected off the California coast from 1975 to 1978. Specimens 1-5 were collected by Sea World of San Diego, no. 6 by K. Skaug and M. Riedman, and no. 7 by an anonymous fisherman.

Specimen number	Date of collection	Location	Sex	Total length (m)	Weight of shark (kg)	Stomach contents
1	24 June 1975	8 km northeast of Santa Catalina Island	F	3.9	623.7	Anterior portion of stomach contained harbor seal remains (18.2 kg). Posterior stomach held unidentified pinniped.
2	1 Aug 1975	110 m west of Laguna Beach	F	2.4	138.8	A 4-in patch of pinniped pelage.
3	6 Sept. 1975	Near Anacapa Island	F	4.9	1,428.8	Harbor seal, well digested.
4	7 Sept 1975	11.3 km southeast of Anacapa Island	F	5.0	1,560.4	Skull and posterior portion of a juvenile elephant seal, plus large amounts of fur and digested material.
5	13 June 1976	West end of Catalina Island	F	5.5	1,882.4	Nearly digested. Bulk suggested a large animal, probably a marine mammal.
6	3 Feb. 1977	Año Nuevo Bay	F	4.7	?	Approximately one-third of a recently eaten 4-yr-old male elephant seal.
7	25 Sept. 1978	1.6 km offshore near Aptos	M	3.9	540	The head of a harbor seal.

other locations along the California coast, was not conducted.

Results

Table 1 summarizes data obtained from the stomachs of seven great white sharks examined shortly after they washed ashore dead or were captured at sea. Four points are worth noting:

1) Six stomachs contained seal remains, three of harbor seals and two of northern elephant seals.
2) Large prey was consumed. On the basis of tooth annuli and head and proboscis size, we estimate that specimen no. 6 (Fig. 1) contained the remains of a male elephant seal, 4 to 5 yr old. Intact, this seal would have measured approximately 3 m in length and weighed 450 to 680 kg.
3) The dimensions of the barely digested material in four of the shark stomachs indicate that the prey had been consumed in large pieces. For example, the stomach of one specimen contained the entire head, unmarred and severed cleanly at the neck. Both hindflippers and the tail were covered with hair and still attached to a segment of the sacrum. Also included were both foreflippers, one attached to a large piece of flesh containing the shoulder, a large portion of the midsection including six vertebrae, and several pieces of flesh and fur in various stages of decomposition. The elephant seal material weighed about 225 kg.
4) Six of the seven sharks were females.

The majority of the shark-injured elephant seals were observed during the winter breeding season. Only two recently bitten animals were observed on Año Nuevo Island in spring, despite the larger number of animals present at this time compared with the breeding season (Le Boeuf and Bonnell 1980).

Fewer than three victims per breeding season were observed from 1968 to 1976. From 1976 to

FIGURE 1.—A moribund great white shark (Specimen No. 6 in Table 1) that washed ashore near Año Nuevo Point shortly after having consumed approximately one-third of a young male northern elephant seal.

1980, 44 elephant seals with shark-inflicted injuries were observed (Table 2). Most of the elephant seals bearing recent shark wounds were adults. Males incurred the highest injury rate. Even the largest adult bulls, measuring more than 4.9 m and weighing between 1,800 and 2,700 kg were observed with shark bites (see Figure 2a). This may be due to the male habit of spending more time in the water near the rookery during the breeding season than females.

TABLE 2.—Shark-bitten northern elephant seals observed on Año Nuevo Island and the Año Nuevo Mainland.

Year	Adult males	Adult females	Juveniles	Pups	Total
1976		3			3
1977	3	4		1	8
1978	1	7	1		9
1979	5	1	1		7
1980	16	1			17
Total	25	16	2	1	44

Shark bites were located on diverse areas of the body but rarely on the head (Fig. 2). Possibly, frontal attacks were less successful or head bitten seals simply did not survive the encounter. In many cases, large pieces of blubber were missing or hung loosely from the animal. Some seals lost a foreflipper or hindflipper and in one case most of the proboscis. Some animals were bitten several times.

The majority of injured seals survived and recuperated rapidly. Infected wounds were rarely observed. Only three elephant seals died on the island or on the mainland following shark injury. In September 1976, an 8½-mo-old female was found dead with numerous deep lacerations and teeth marks covering her body. In December 1977, a 1-wk-old pup washed up with its entire sacral region amputated just below the umbilicus. In February 1978, a large 7-yr-old male died on the island's main breeding beach from massive shark wounds incurred within the previous 24 h. The most serious wounds consisted of two large oval chunks of flesh missing from the left side of the thoracic region (Fig. 2e). The bites measured 61 and 69 cm wide, 61 cm high, and 30 cm deep. No bite penetrated the body cavity although some muscle was removed and a rib was partly exposed.

Most female elephant seals bitten by sharks shortly before giving birth failed to wean their pups successfully. One female gave birth to a stillborn and returned to sea immediately. Seven females either abandoned their pups shortly after parturition or they were unable to care for them adequately. Four of these pups died; the eventual status of the other three pups could not be determined. The three females who were successful in weaning their pups appeared to have sustained the least serious injuries. All injured females remained in the harem for a much shorter period than normal. No injured female was observed to copulate, as uninjured females do, just before returning to sea. Thus, most injured females not only failed to produce a pup during the year of injury, but if they failed to copulate, they did not reproduce in the subsequent year as well.

Discussion

The data on stomach contents of white sharks presented in this paper is conclusive evidence that this shark preys on elephant seals and harbor seals in southern and central California waters.

We hypothesize that shark-inflicted injuries to northern elephant seals at Año Nuevo were caused primarily by white sharks. This hypothesis is supported by:

1) Data from a white shark that washed ashore at Año Nuevo Bay whose stomach contained the remains of an elephant seal (Table 2).
2) Observation of white sharks in the area. Twice during the summer of 1970 seal researchers saw white sharks measuring about 4.5 m from a dinghy 100 m south of the island. Party boat operators and fishermen reported seeing white sharks in this area several times during the last decade. Anglers report that white sharks occasionally attack large lingcod, *Ophidon elongatus*, when they are caught on hook and line; the sharks surface and circle boats, especially when fishing stops (Miller and Collier 1980).
3) An observed white shark attack of a northern elephant seal near Año Nuevo Island. This occurred on 1 February 1981.
4) The large size of shark bites. This indicates that they were caused by large sharks. White sharks may also be responsible for injuries to elephant seals on other rookeries in California (Ainley et al. 1981) and in Mexico (Townsend 1885; B. Le Boeuf, pers. obs.).

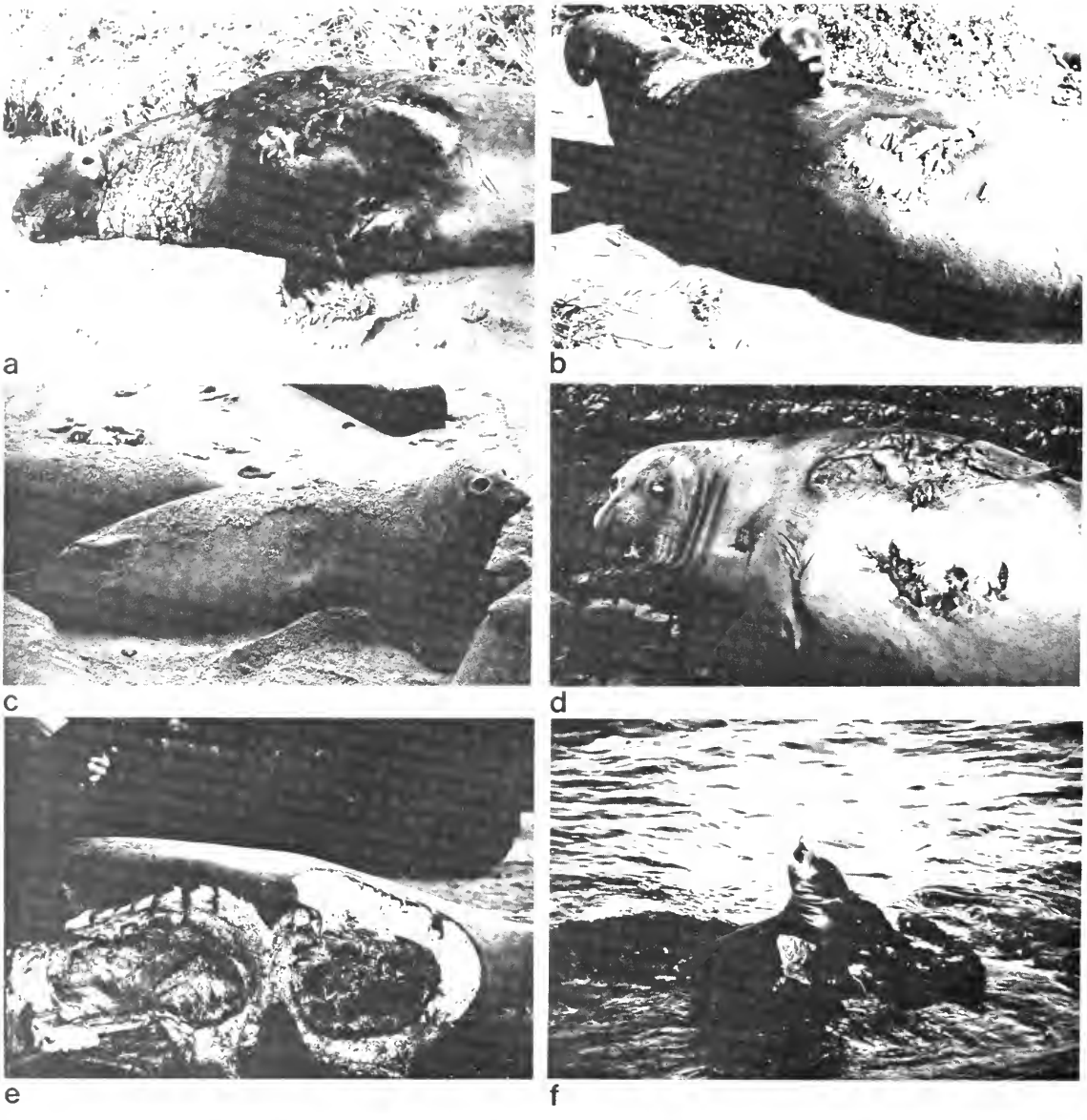

FIGURE 2.—A variety of shark-inflicted wounds observed on elephant seals and sea lions at Año Nuevo. A crescent shaped wound (a) and toothprints (b) on adult male elephant seals. A crescent bite on the dorsal posterior of an adult female elephant seal (c) and a large imprint of both jaws on an adult female with a blind left eye (d). Two large chunks of flesh bitten off the left side of an adult male elephant seal who subsequently died from his wounds (e). A California sea lion bearing a recently inflicted shark injury (f).

The results of this study support and augment those of Ainley et al. (1981) on South Farallon Island near San Francisco, Calif. They found that white sharks were responsible for most of the shark attacks observed on pinnipeds in the waters surrounding the island during the period September 1970 to February 1979. Northern elephant seals were attacked more frequently than harbor seals and sea lions, and shark-bitten female elephant seals exhibited low reproductive success.

Shark attacks on elephant seals of Año Nuevo Island and South Farallon Island (Ainley et al. 1981) appear to be increasing, but more data

based on continued monitoring is necessary to confirm this point. Periodic increases in shark attacks of the magnitude found in these two studies may be related to several possible factors: The well-documented increase in elephant seals (Le Boeuf and Bonnell 1980), an increase in abundance of sharks, or to one or a few relatively inept predators at work.

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VERTICAL STRATIFICATION OF THREE NEARSHORE SOUTHERN CALIFORNIA LARVAL FISHES (*ENGRAULIS MORDAX*, *GENYONEMUS LINEATUS*, AND *SERIPHUS POLITUS*)

Length measurements of larval fish are most frequently used in describing life stages (Moser and Ahlstrom 1974), and the subsequent development of population estimates (Kumar and Adams 1977). Field and laboratory observations are used to construct growth models of larval fishes, which are useful in predicting rates of growth under various environmental conditions (Hunter 1976). When combined with observations of larval abundance and distribution, length measurements can be indicators of both larval and adult ecology. Larval length-frequency data provide information about adult distribution and abundance, spawning periodicity, food preferences, and behavioral transitions that occur during development (Gjøsaetor and Saetre 1974; Tanaka 1974).

Larval length-frequency distributions of three species of fish were determined in conjunction with a study of the effects of a power plant offshore cooling water intake on local nekton populations. The three species chosen [northern an-

chovy, *Engraulis mordax* (Engraulididae); white croaker, *Genyonemus lineatus* (Sciaenidae); queenfish, *Seriphus politus* (Sciaenidae)] are among the most abundant adult fishes in the area, and are important links in the local trophic structure. The northern anchovy is important as forage for larger fishes and is fished commercially for manufacture of fish meal and oil. While the two sciaenid species have less commercial value, both are important as forage for larger species.

Materials and Methods

Samples were collected as part of a program of preoperational environmental studies at San Onofre Nuclear Generating Station (Fig. 1). In the area near the generating station (designated "treatment"), two transects extended over depths of 8 to 11 m and 12 to 15 m. Transects were also located in a "reference" area 5.8 km northwest. The two areas are similar in bottom topography and in the presence of a kelp bed just south of the outer transects. Each transect was 760 m in length. The two treatment transects and the two reference transects were each separated by 150 m. Monthly collections were made every 30±2 d from March 1978 through July 1979. Results for March through July samples for 1978 and 1979 are presented as mean values for the 2 yr combined.

Three vertical water column levels were sampled. The neuston was sampled, using a Manta net (Brown 1979). This net has a rectangular mouth (86 cm × 15 cm) and is designed to sample the upper 14 cm of the water column. The net filtered a volume of approximately 100 m^3 during each tow.

Midwater samples were taken with paired opening-closing 60 cm diameter circular bongo

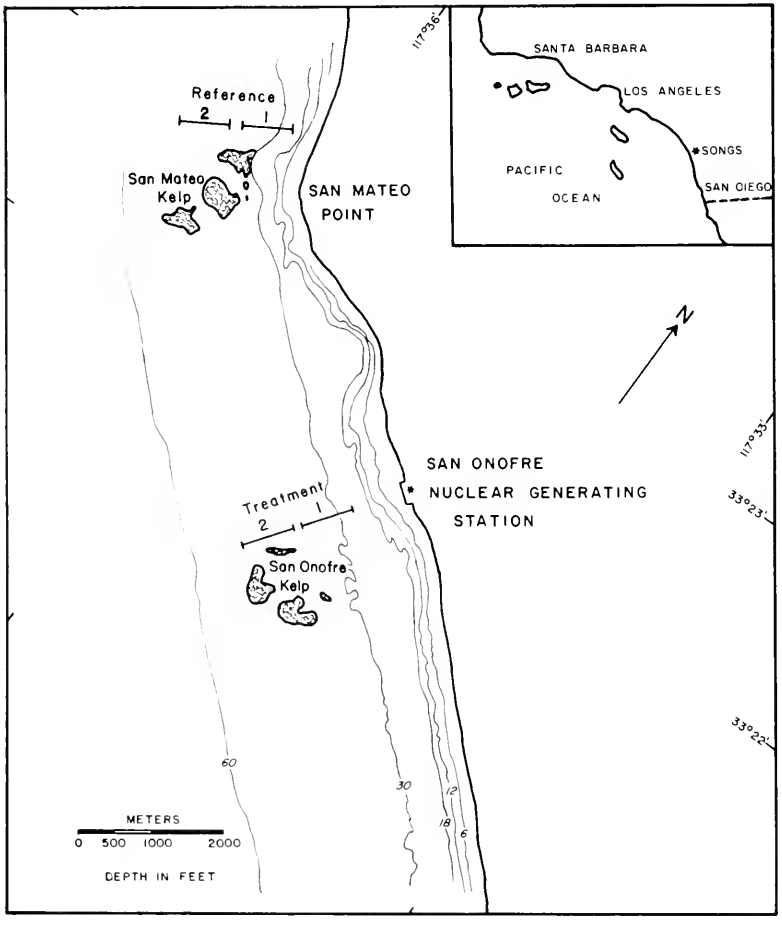

FIGURE 1.—Location of sampling stations offshore San Onofre Nuclear Generating Station ("treatment") and San Mateo Point ("reference"). Inset locates the area in relation to southern California.

nets (McGowan and Brown 1966) towed obliquely through the entire midwater column (about 0.5 m below the surface to 1.0 m above the bottom). Each side of the paired net filtered a volume of about 200 m^3/tow.

Samples from the epibenthos were collected using an Auriga[1] net specially designed for sampling over rock-cobble bottoms. The net has a rectangular mouth, 0.5 m × 2.0 m, and filtered about 800 m^3 during each tow.

Each net was equipped with two flowmeters for volume determinations. Mesh size of each net was 0.333 mm, to facilitate collection of both eggs and larvae (Bolin 1936). Four replicates were collected by each gear at night at each of the four transects.

Due to shrinkage of the larvae during preservation (4% buffered Formalin-seawater), lengths of the individuals at hatching were smaller than those observed for unpreserved specimens (Theilacker 1980), ranging from 1.9 mm for white croaker to 2.5 mm for northern anchovy. The fish were considered to become juveniles after the development of adult fin rays and spines, which was taken as a length of 30 mm for all three species. Larvae were divided into 10 size classes of 3 mm each.

Results

Engraulis mordax

The major spawning period for northern anchovy was observed to be from December through May (Fig. 2). Length-frequency distributions in neuston samples indicated a pattern of high concentrations of small larvae during heaviest spawning periods (March and December 1978), followed by months of relatively even distributions from 0 to 15 mm. Larger larvae appeared and often became the major larval component in the neuston 2 to 3 mo after heavy spawning periods. Midsize larvae (12 to 18 mm) were often observed in reduced numbers in comparison with smaller or larger larval sizes. Low spawning activity during late summer was reflected in reduced numbers of larvae in neuston samples.

Midwater collections of northern anchovy were characterized by larval concentrations in the 6 to 18 mm size range, with abundance of 0 to 6 mm larvae fluctuating with spawning activity of adults. Except in the heavy spawning months of March and December 1978, midsize larvae generally outnumbered 2.5 to 6 mm larvae and composed the majority of midwater larvae taken. Significant numbers of larvae >21 mm were taken in the midwater samples only at the end of the main spawning season.

Collections of northern anchovy from epibenthic samples indicate consistent dominance of the distribution by 6 to 18 mm larvae during most months, with distributions shifted toward larger larvae during midsummer months. Overall concentrations in epibenthic samples were consistently the highest among the three levels.

Genyonemus lineatus

The major spawning period for white croaker was from December to May (Fig. 3). Larvae taken in the neuston were generally low in abundance and rarely larger than 6 mm, while midwater concentrations were also generally restricted to 0 to 6 mm larvae. Larvae were observed in these levels mainly from December through April. Most white croaker larvae were taken in epibenthic samples, especially late in the spawning season. In contrast to the upper two levels, larvae were relatively abundant from October through June. While small larvae were frequently taken in epibenthic samples during the major spawning months, the epibenthos was generally dominated by larvae in the 3 to 12 mm size range. Larvae >15 mm were rarely taken.

Seriphus politus

Queenfish, like white croaker, is highly seasonal in its spawning habits, with the main spawning period extending from March to September (Fig. 4). Significant numbers of larvae were taken in neuston collections only in March and April, and were restricted to 0 to 6 mm size classes. Midwater collections followed a similar trend, although slightly larger larvae persisted through September. The majority of queenfish larvae were taken in epibenthic samples, with numbers of individuals in each size class decreasing from 0 to 3 mm through 15 to 18 mm groups. As was observed in white croaker samples, individuals >18 mm were rarely collected.

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

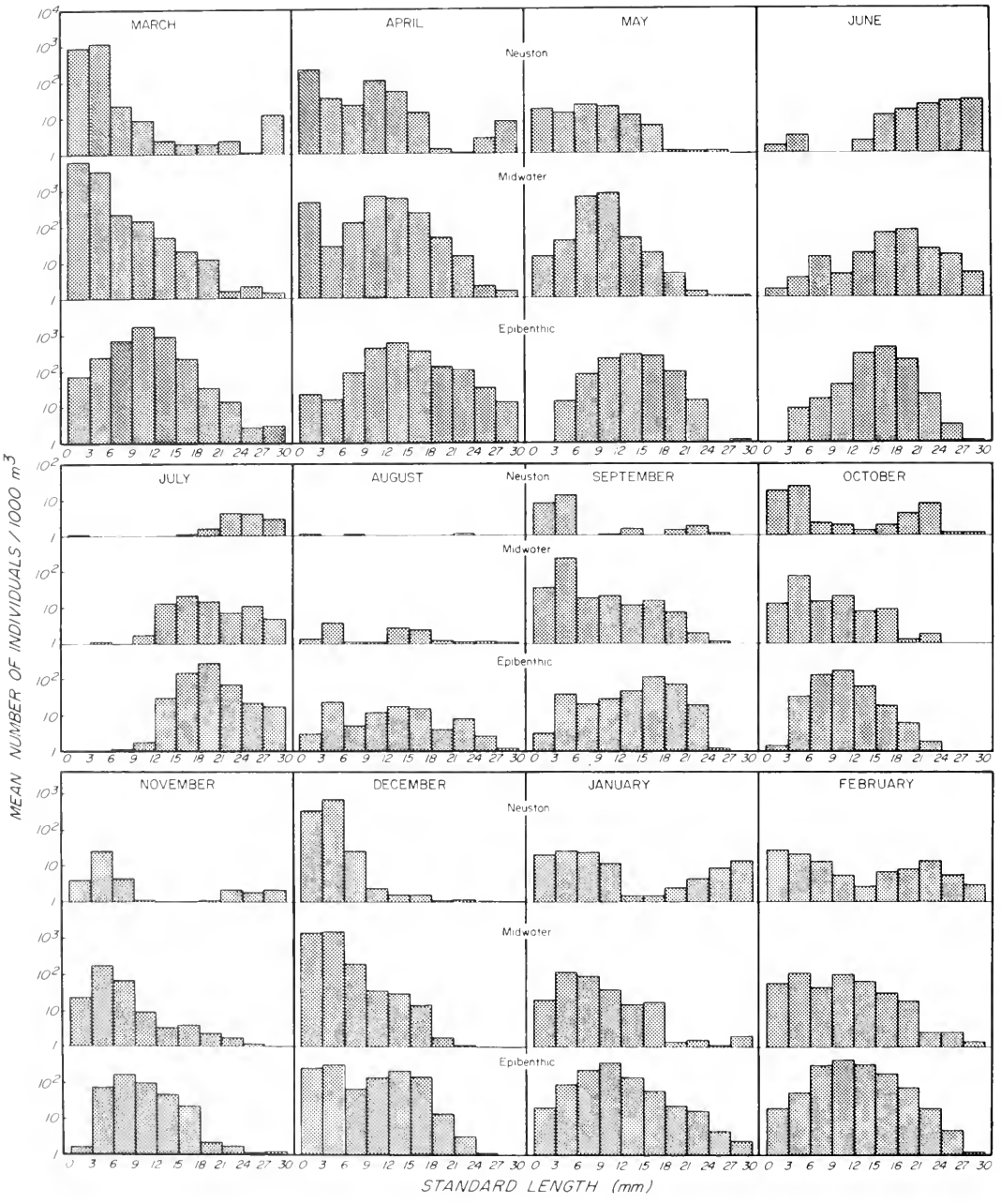

FIGURE 2.—Mean monthly concentrations of 10 larval size classes of northern anchovy, *Engraulis mordax*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

Discussion

In preliminary studies near San Onofre from August 1977 through February 1978, significantly greater numbers of larvae were observed in all three water column levels at night compared with daytime collections. Sampling was restricted to nighttime beginning in March 1978.

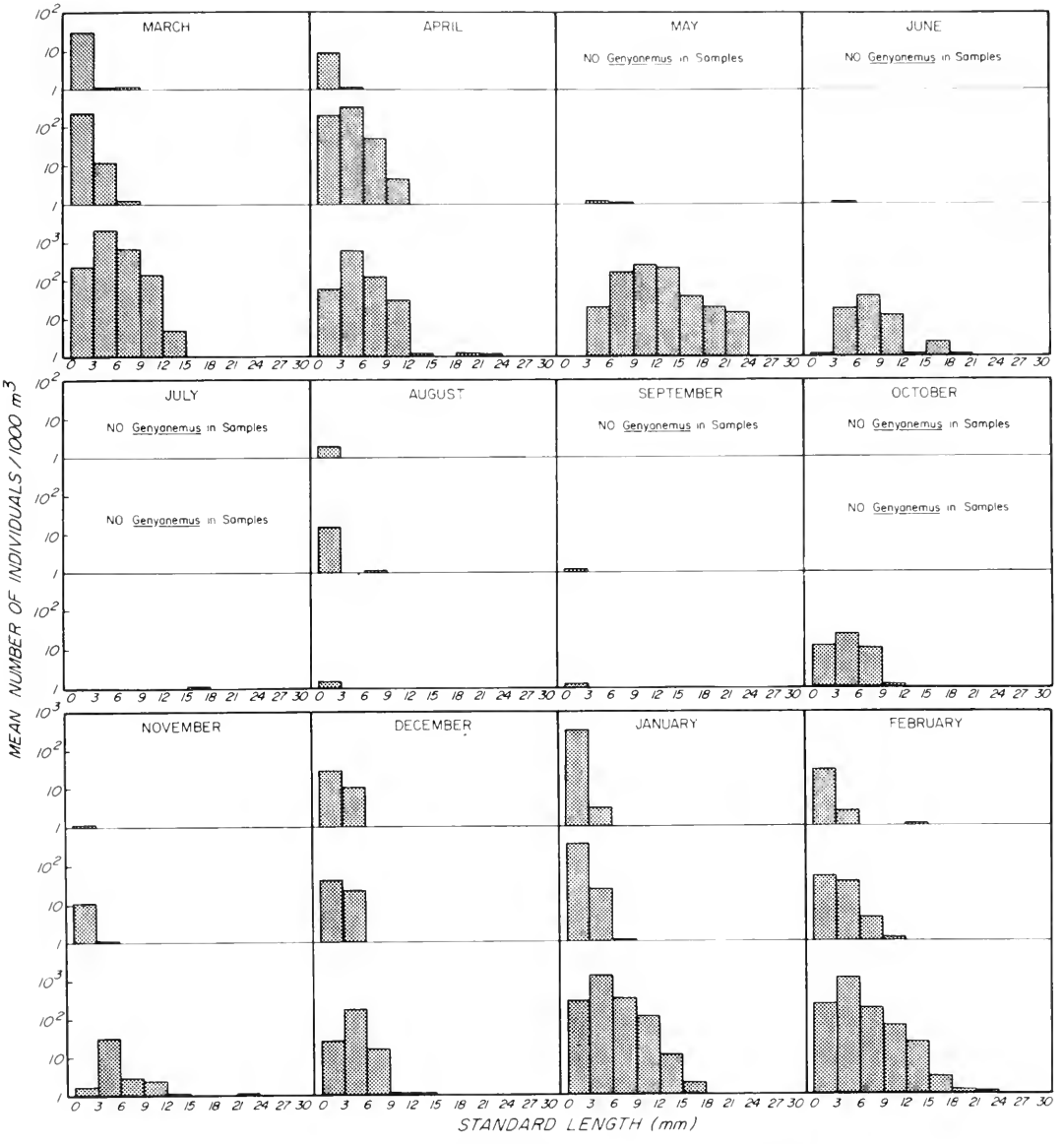

FIGURE 3.—Mean monthly concentrations of 10 larval size classes of white croaker, *Genyonemus lineatus*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

During the course of the study, no relationship between larval abundance and distribution and tidal stage, sea state, or stage of the moon was noted.

Vertical length-frequency distributions of all three species examined appear to be related to mode of feeding of each larval species, development during life history, and availability of food in the study area. The relationship between food availability and survival of larval northern anchovy is well documented. Larval anchovy require cells of 40 μm diameter in concentrations near 30 particles/ml (Lasker 1975, 1978). Lasker (1975) observed extensive feeding of anchovy larvae at the chlorophyll maximum layer, and Hunter and Thomas (1974) stated that anchovy

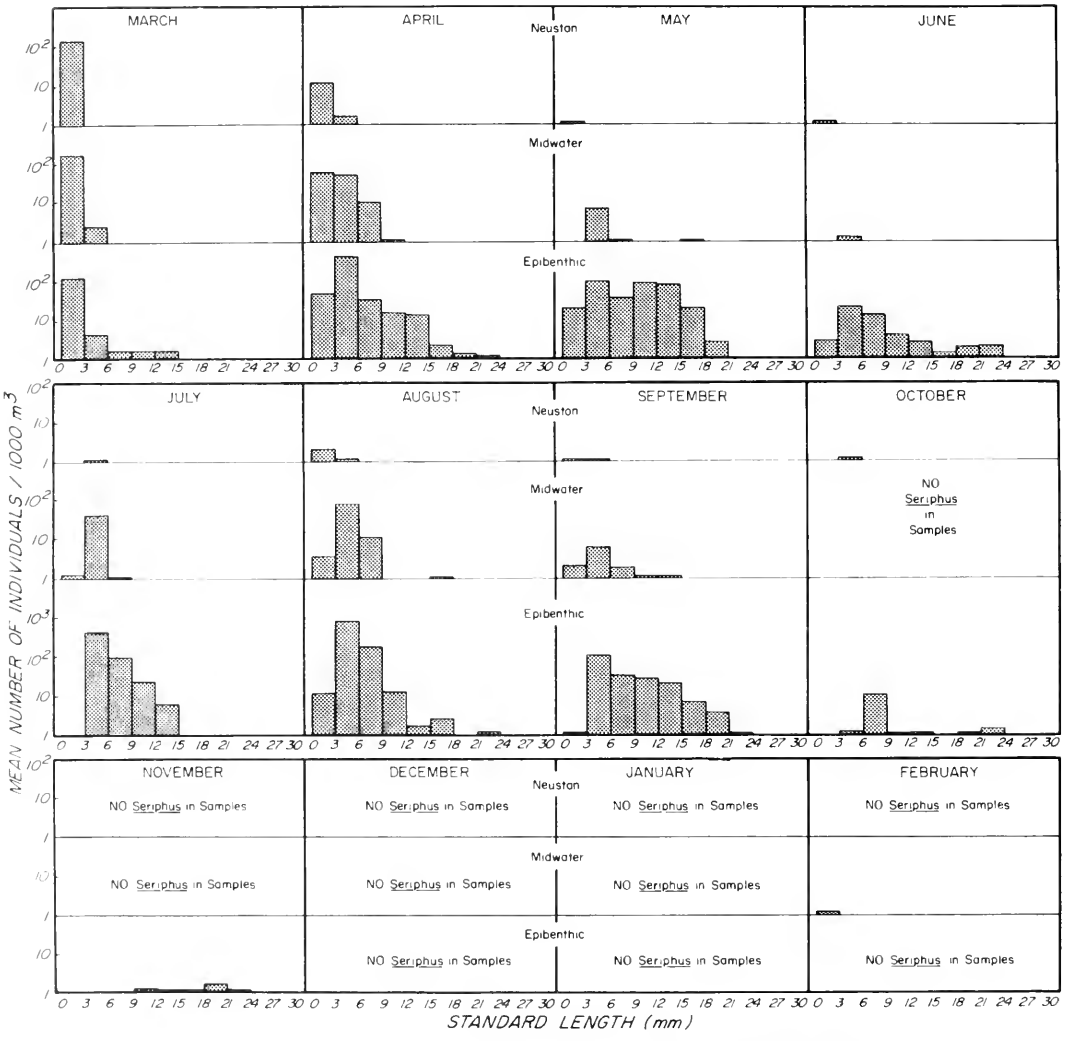

FIGURE 4.—Mean monthly concentrations of 10 larval size classes of queenfish, *Seriphus politus*, in three water column levels, March 1978-February 1979. Each monthly value represents a mean of 4 replicates from each of 4 transects (total replicates = 16).

larvae seek and remain in patches of the dinoflagellate *Gymnodinium splendens* in both day and night. Vertical differences in anchovy larval concentrations were shown by Ahlstrom (1959) to correspond to the level of the thermocline. In the San Onofre nearshore region, the maximum depths of the sampled transects were only 11 to 15 m, and the vertical zone is substantially compressed compared with offshore waters. Studies have indicated high concentrations of food in this nearshore area (Barnett and Sertic 1979). Concentrations of chlorophyll a 1 m below the surface and 1 m above the bottom were nearly equal during all times of the year from August 1976 to September 1978 at depths of 7 to 8 m and 18 to 30 m off San Onofre. Because adequate food may exist throughout the water column, a range of size classes is encountered at all depths. The apparent downward movement of larger anchovy larvae appears to be a natural behavioral response.

White croaker and queenfish larvae migrate toward the bottom after hatching. This vertical movement is associated with their adult life his-

tory, which is benthic in nature (Goldberg 1976). Additionally, larvae of 3 to 15 mm length of both these species feed primarily on zooplankton, which have been shown to be most abundant near the bottom in the nearshore San Onofre area (Barnett and Sertic 1979).

The absence of queenfish larvae in the neuston during the summer, and low concentrations in the midwater compared with the epibenthic level during the same period, may be due to the formation of the thermocline (density gradient) preventing eggs from entering the upper water column prior to hatching. Larvae of *G. lineatus* are more prevalent in these levels during the winter, when the water column is well mixed.

Length-frequency distributions of all three larval species are dependent on spawning cycles and behavioral and feeding patterns. Length-frequency distributions are reasonably accurate indicators of spawning periods, dependent on the life history of the species in question. Larvae of larger size classes are generally prevalent during periods of lowest abundance, after the main spawning period ends. During spawning periods, the distribution is dominated by smaller larvae. In distributions of northern anchovy, which apparently spawns intermittently year-round in the San Onofre region, the variability of the length-frequency median from month to month is highest in the neuston net and lowest in the epibenthos. Northern anchovy larvae apparently migrate from the neuston soon after hatching, but return upon reaching lengths of about 20 mm. Superimposed on spawning cycles, this phenomenon induces a high degree of variability to length-frequency medians of neuston samples. Larvae of the two sciaenid species, however, are benthic in nature, leading to increased variability in epibenthic samples, where the majority of these larvae are collected. At any one time, the major determining factor regulating the length-frequency distribution of these larval species near San Onofre is the reproductive state of each of the species.

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DECREASE IN LENGTH AT PREDOMINANT AGES DURING A SPAWNING MIGRATION OF THE ALEWIFE, *ALOSA PSEUDOHARENGUS*[1]

The spawning migration of the anadromous alewife, *Alosa pseudoharengus*, has been characterized by a decreasing trend in size and age. Cooper (1961) reported a trend in decreasing size in Pausacaco Pond, R.I., and Kissil (1974) found this one year in a 2-yr study at Bride Lake, Conn. A trend of decreasing size and age composition was also found in the Damariscotta River, Maine, alewife migration for the years 1977 through 1979 (Libby 1981).

Since 1977, data have been collected for length, weight, sex, age, and daily catch from the Damariscotta River commercial fishery. Analysis resulted in length-weight relationships, length, sex and age compositions, and an overall view of the annual stock changes. Further analysis of the collected data revealed that as age of the alewives decreased during migration, lengths at age also decreased with time. The analysis was applied only to 1979 and 1980 because of insufficient data in the other years.

The intent of this paper is to show the analysis and explain in greater detail this trend in decreasing length at age of an alewife migration.

The Study Area

The Damariscotta River alewife fishery is located approximately 29 km from the mouth of the river at the head of tide (Fig. 1). The river terminates at Great Salt Bay where a small outflow stream connects it with Damariscotta Lake.

Alewives are harvested with traps consisting of moveable metal bins that are set into the stream. Alewives swim into these bins which are then hoisted out of the water and the fish are dumped into a holding trough. The alewives that escape capture may pass through a fishway and

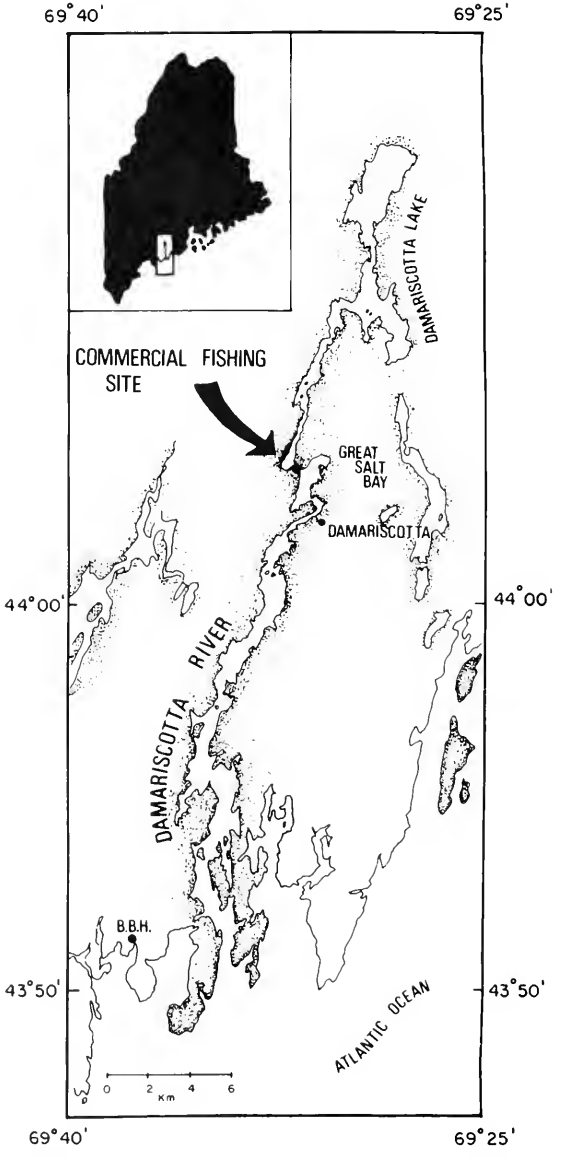

FIGURE 1.—Damariscotta River and site of the commercial alewife fishery.

[1]This study was conducted in cooperation with the U.S. Department of Commerce, National Marine Fisheries Service, under Public Law 89-304, as amended, Commercial Fisheries Research and Development Act, Projects AFC-21-1 and AFC-22-2.

into the lake to spawn. This particular fishery is one of about 30 commercially harvested alewife runs on the Maine coast and produces between 20 and 30% of the state's landings.

Materials and Methods

The method of harvesting was not considered selective of size, sex, or age of the alewives, and the catch presumably represented the true composition of the migrating stock. From previous work it was known that the size and age composition was not homogeneous throughout the run (Libby 1981), so a catch sample of fish was taken on alternate days to gain an equal representation of the total run.

Each sample consisted of 50 fish scooped from the catch in the holding trough. The sample was then brought to the laboratory and processed as soon as possible to minimize shrinkage or weight loss. Total length and weight were measured to the nearest millimeter and 0.1 g, respectively. The alewives were sexed by visual inspection of the gonads.

Otoliths were removed, cleaned, dried, and set into labeled black Plexiglas[2] trays. Watson (1965) described this procedure for mounting otoliths with the use of ethylene dichloride to fix the otoliths permanently in the trays. I prefer Permount, a histological medium that is poured over the otoliths and left to harden. If an otolith has to be repositioned, a drop of xylene will dissolve the Permount back to a liquid state. The otoliths were read with the use of a binocular microscope at a 30×-60× magnification.

Results and Discussion

The 1980 commercial harvest for the Damariscotta River lasted for 34 d, starting 4 May and ending 6 June. Fifteen daily samples were taken, each sample containing about 50 alewives totaling 365 males and 346 females. In each sample the sex ratio did not deviate significantly ($P > 0.05$) based on a χ^2 test from a 1:1 ratio (Table 1). This ratio had been previously shown to be consistent from 1977 to 1979 in the Damariscotta River (Libby 1981).

In analyzing length with time, I was more concerned with similarities between the slopes of lines comparing males and females than in differences between mean lengths. Using the 1980 data as an example, females were shown to be larger than males at a given age (Table 1). A covariance analysis (Table 2) revealed no significant differences between slopes of the lines for the two sexes at the 5% level. Even though the mean length varied daily, the compared length distribution in each sample was less variable. Bartlett's test of homogeneity demonstrated no significant differences between the residual variances ($\chi^2 = 3.59$, df = 1, $P > 0.05$). A t-test of significance of slope (t equals a ratio of the slope to its standard error) applied to the pooled regression coefficient showed that the slope (−0.36) was significantly different from zero ($t = 9.36$, df = 707, $P < 0.05$). The influx of male and female alewives into the river follows a similar pattern regardless of their size differences. Ages throughout the 1979 and 1980 samples ranged from 3 to 8 yr for 234 males and 3 to 9 yr for 259 females and from 4 to 7 yr for 361 males and 3 to 7 yr for 344 females, respectively.

TABLE 1.—Sex ratios and mean length of 15 alewife samples taken from the 1980 Damariscotta River commercial fishery.

Date	Sex ratio M:F	No. sampled	Mean length			
			Males	SE	Females	SE
5/6	1.3:1	50	305.0	1.7	316.2	2.2
5/8	1.0:1	50	300.4	1.8	316.6	1.6
5/12	1.1:1	50	305.2	1.7	310.2	2.0
5/14	1.2:1	50	304.1	1.6	315.4	2.3
5/16	0.9:1	37	304.4	1.6	312.9	2.2
5/18	0.6:1	50	301.6	1.8	308.5	1.6
5/20	1.2:1	50	299.9	1.5	311.0	1.4
5/22	1.4:1	50	302.0	1.4	309.0	1.8
5/24	0.8:1	50	292.7	1.8	302.0	1.7
5/26	0.9:1	50	299.3	1.5	308.3	1.8
5/28	1.3:1	50	296.3	1.7	305.9	2.5
5/30	0.9:1	50	295.7	1.7	304.2	1.8
6/1	1.1:1	45	298.0	1.9	307.7	2.2
6/3	1.2:1	44	293.4	2.2	307.2	2.3
6/5	1.5:1	35	299.0	2.7	305.3	2.4

TABLE 2.—Analysis of covariance of length by time regression for male and female alewives and test for nonzero pooled slope, Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Males	−0.32	363	27,388.279	
Females	−0.40	344	31,754.933	
	within	707	59,143.212	83.65
Pooled	−0.36	708	59,217.604	
Difference between slopes		1	74.392	74.39
Comparison of slopes		[1]F = 0.89, df = 707 [2]P = 0.65		
Test of pooled slope coefficient		[3]B = −0.36 SE = 0.04 $t = B/SE = 9.36$		

[1]F test, ratio of mean square of difference between slopes to mean square of difference within slopes.
[2]Calculated probability, not significant at the 5% level.
[3]Pooled slope coefficient.

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

Age distribution from the 1979 and 1980 samples

Age:	3	4	5	6	7	8	9	Total
1979								
Males	5	134	79	11	4	1	—	234
Females	1	115	116	22	3	1	1	259
1980								
Males	—	116	221	22	2	—	—	361
Females	2	93	211	32	6	—	—	344

Age by time regressions for the 1980 data were computed for each sex and an analysis of covariance (Table 3) revealed no significant differences between the slopes. The pooled regression like the pooled length by time regression, showed a significant slope (−0.02) at the 5% level. These two nonzero slopes (length by time and age by time) are evidence of changes in mean size and mean age throughout this alewife migration. The slope of the length trend (−0.36) is greater and significantly different from the age trend slope (−0.02) at the 5% level. The daily age composition of alewives moving to their spawning ground is a result of the fish schooling by size.

Lengths were separated into respective age categories for both years and regressions were computed of the age-length relation over time for each sex (Fig. 2). This was not done for ages three and seven through nine because of the small sample size. Ages four, five, and six were predominant, constituting over 95% of all the fish in the samples. All regressions produced negative slopes, although regressions A and B in 1979 and C and D in 1980 (Fig. 2) proved their slopes to be nonsignificant from a zero slope.

An analysis of covariance applied to all regressions in each year showed no significant differences between slopes (Tables 4, 5). Apparently

TABLE 3.—Analysis of covariance of age by time regressions for male and female alewives and test for nonzero pooled slope. Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Males	−0.016	359	115.755	
Females	−0.021	342	137.007	
	within	701	252.872	0.36
Pooled	0.019	702	253.127	
Difference between slopes		1	0.365	0.37
Comparison of slopes		[1]F = 1.01, df = 701 [2]P = 0.32		
Test of pooled slope coefficient		[3]B = 0.02 SE = 0.003		
		t = B/SE = 7.49		

[1]F test, ratio of mean square of difference between slopes to mean square of difference within slopes.
[2]Calculated probability, not significant at the 5% level.
[3]Pooled slope coefficient.

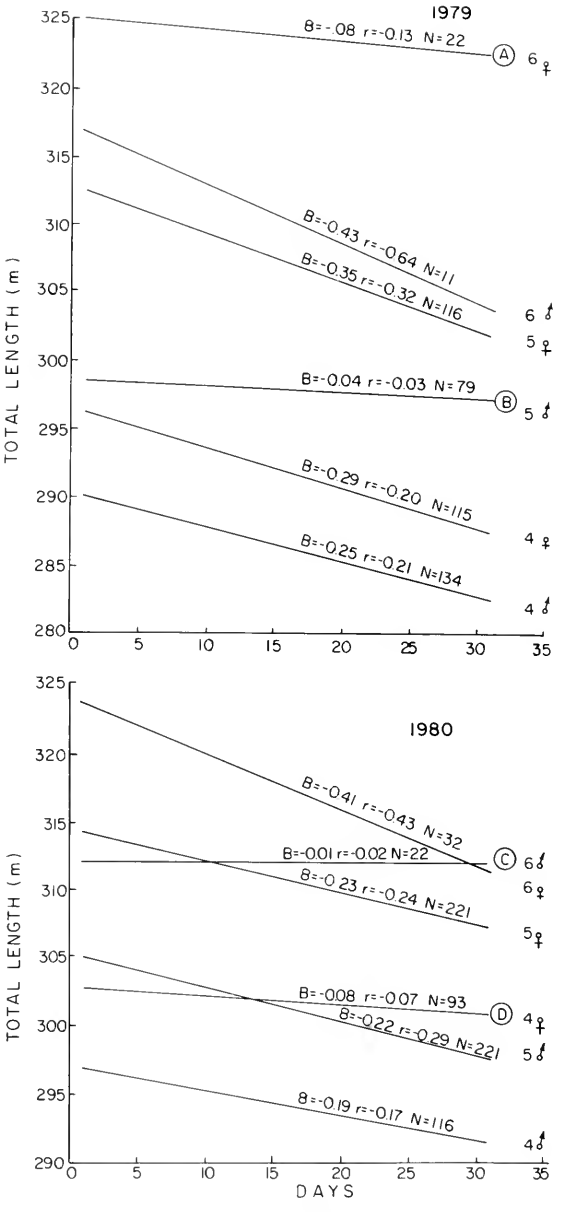

FIGURE 2.—Regressions of length at age with time from the 1979 and 1980 Damariscotta River alewife fishery.

the nonsignificant slopes still contributed to the homogeneity of the combined slopes producing significant 1979 and 1980 pooled regression slopes of −0.24 and −0.21, respectively. These results show, along with the previously observed decrease in length with time and age with time of this alewife migration, that the length of fish at age also decreases with time. The fish that arrive

TABLE 4.—Analysis of covariance of length by time regression by age and sex for alewives and test for nonzero pooled slope. Damariscotta River, 1979.

Treatment	Regression coefficient	df	Residual SS	Mean square
Male age				
4	−0.25	132	12,772.315	
5	−0.04	77	9,186.425	
6	0.42	9	269.782	
Female age				
4	−0.29	113	11,810.600	
5	−0.35	114	11,923.360	
6	−0.08	20	996.642	
	within	465	46,959.124	100.10
Pooled	−0.24	470	47,503.000	
Difference between slopes		5	543.876	108.7
Comparison of slopes		[1]F = 1.07, df = 465 [2]P = 0.63		
Test of pooled slope coefficient		[3]B = −0.24 SE = 0.05		
		$t = B/SE = 4.59$		

[1]F test, ratio of mean square of difference between slopes to mean square of difference within slopes.
[2]Calculated probability, not significant at the 5% level.
[3]Pooled slope coefficient.

TABLE 5.—Analysis of covariance of length by time regressions by age and sex and test for nonzero pooled slope. Damariscotta River, 1980.

Treatment	Regression coefficient	df	Residual SS	Mean square
Male age				
4	−0.19	114	7,819.279	
5	−0.22	219	10,575.189	
6	−0.01	20	835.044	
Female age				
4	−0.08	91	5,926.716	
5	−0.24	210	14,708.805	
6	−0.41	30	1,699.554	
	within	683	41,564.587	60.86
Pooled	−0.21	688	41,824.344	
Difference between slopes		5	259.757	51.95
Comparison of slopes		[1]F = 0.854, df = 683 [2]P = 0.49		
Test of pooled slope coefficient		[3]B = −0.21 SE = 0.03		
		$t = B/SE = 6.15$		

[1]F test, ratio of mean square of difference between slopes to mean square of difference within slopes.
[2]Calculated probability, not significant at the 5% level.
[3]Pooled slope coefficient.

earliest are not only the largest of the migrating stock but also of the age groups.

The change in length at age is a source of bias in determining the age composition of the alewife harvest if a pooled age-length key were used. Westrheim and Ricker (1978) studied biases connected with application of an age-length key to stocks with different age compositions. Using an age-length key derived from pooled length subsamples will introduce bias in computing age composition of an anadromous alewife run. The pooled age-length key assumes homogeneity, but lengths at age change throughout the migration period. Such bias may, however, dwell within the range of acceptable error of 5% of the expected age frequencies. Chi square applied to each observed age frequency against the age-length key expected frequency, for each day sampled, indicated no significant differences between observed and expected age frequencies in the 1980 data. The magnitude of this decreasing trend in length at age may vary from year to year and stock to stock, but it is present and should be taken into account when investigating a migratory stock of alewives.

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SEASONAL SPAWNING CYCLE OF THE LONGFIN SANDDAB, *CITHARICHTHYS XANTHOSTIGMA* (BOTHIDAE)

This note contains the first description of the seasonal spawning cycle of the longfin sanddab, *Citharichthys xanthostigma*. This fish is common off southern California, but rare north of Santa Barbara and occurs at depths from 2 to 201 m (Miller and Lea 1976).

Methods

Fish were collected by otter trawl off the coast of southern California at depths of 45-64 m from San Clemente (lat. 33°20'N, long. 117°38'W) to Huntington Beach (lat. 33°40'N, long. 118°00'W). Collections were made during January-December 1978. Only females were examined. Specimens were immediately slit along the abdomen and placed in 10% Formalin[1]. Ovarian histological sections from 137 *C. xanthostigma* were cut at 8 μm and stained with iron hematoxylin. Seasonal gonosomatic indices (ovary wt/fish wt × 100) were calculated from preserved fish. Ovaries were classified histologically into four stages (Table 1).

TABLE 1.—Monthly distribution of body sizes (SL) and stages in *Citharichthys xanthostigma* spawning cycle, January-December 1978.

Month	*N*	Range (mm)	Regressed or regressing (%)	Previtellogenic (%)	Vitellogenic (%)	Spawning (%)
January	12	127-162	8	0	0	92
February	17	107-162	0	6	6	88
April	14	144-190	79	0	0	21
May	17	115-180	82	0	0	18
June	20	110-181	95	0	0	5
July	21	137-210	100	0	0	0
October	18	116-190	44	28	28	0
December	18	115-160	17	17	11	55

Results

Most *C. xanthostigma* spawn in winter (Table 1). At this time the majority of females contain yolk-filled oocytes (>290 μm in diameter) and gonosomatic indices reach their highest values (Fig. 1). Females were in spawning condition in December. The presence of mature (yolk-filled) oocytes from an incipient spawning, and of postovulatory follicles which are remnants of the follicular walls of recently spawned oocytes (Hunter and Goldberg 1980), and of maturing oocytes for a subsequent spawning in the same ovary indicated that *C. xanthostigma* spawns more than once each season. The number of spawnings per season is unknown, however. Postovulatory follicles were similar to those of other teleost fishes (Hunter and Goldberg 1980). The smallest mature (ripe) female measured 107 mm SL (standard length); the largest, 181 mm SL. Miller and Lea (1976) reported this species may reach 250 mm TL (total length).

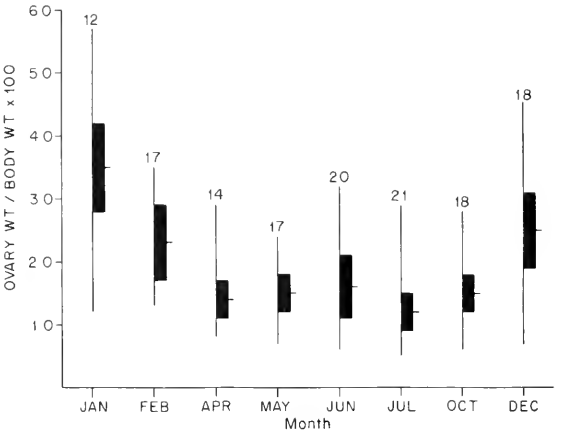

FIGURE 1.—Seasonal gonosomatic indices for *Citharichthys xanthostigma*. Vertical line = range; horizontal line = mean; rectangle = 95% confidence interval. Sample size above each month.

The incidence of spawning females decreased in spring. At this time most females contained regressed ovaries (Table 1) consisting of primary oocytes (53 μm) or regressing ovaries in which oocytes in various stages of vitellogenesis were undergoing atresia. Ovaries from fish taken during July were regressed, and gonosomatic indices were reduced (Fig. 1). Ovarian activity for the new spawning cycle began during autumn. This was apparent in October (Table 1) when previtellogenic females containing slightly enlarged, vacuolated oocytes (118 μm) and vitellogenic females (yolk deposition in enlarging oocytes) were present.

Discussion

My data have shown *C. xanthostigma* is a winter spawner in southern California. Spawning

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

times in other California flatfishes are variable with a tendency toward winter. Fitch and Lavenberg (1971) reported the following spawning periods: *Platichthys stellatus*, November-February; *Microstomus pacificus*, November-March; *Citharichthys sordidus*, July-September; *Paralichthys californicus*, February-July. Goldberg (1981) reported summer spawning in *Symphurus atricauda* and summer-fall spawning (Goldberg 1982) in *Hippoglossina stomata*. Spawning in *Citharichthys stigmaeus* occurs April-September (Ford 1965). *Pleuronichthys verticalis* which was investigated by Fitch (1963) and Goldberg (1982) and *Glyptocephalus zachirus* which Frey (1971) reported on were in spawning condition throughout the year. Such year-round spawning is uncommon among California flatfishes.

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OTTER TRAWL SAMPLING BIAS OF THE GILL PARASITE, *LIRONECA VULGARIS* (ISOPODA, CYMOTHOIDAE), FROM SANDDAB HOSTS, *CITHARICHTHYS* SPP.

Lironeca vulgaris (Crustacea, Isopoda, Cymothoidae) is a common parasite infesting the gill chambers of many marine fish species from the California coast. Both male and female isopods reside in the gill chambers of sanddab hosts. Aspects of the ecology of this parasite and host specificity are given in Brusca (1978, 1981) and Keusink (1979). Both authors discuss the propensity of isopods, particularly males, to abandon hosts in otter trawls, which may cause false host records. Further, if host abandonment occurs during the trawling operation then estimates of prevalence (no. of infested hosts/total no. of hosts), relative parasite density (total no. of parasites/total no. of hosts), and mean parasite intensity (total no. of parasites/no. of infested hosts) will be biased. During a study of the interactions between *L. vulgaris* and two sanddab hosts, *Citharichthys stigmaeus* and *C. sordidus*, I analyzed the efficiency of traditional otter trawl collecting methods. Prevalence, relative parasite density, and mean parasite intensity were compared for samples of a host population gathered by otter trawls and divers utilizing scuba.

Methods

Speckled sanddabs, *Citharichthys stigmaeus*, and Pacific sanddabs, *C. sordidus*, were collected from a site about 0.5 km west of Goleta Point, Santa Barbara County, Calif., just seaward of an extensive bed of giant kelp, *Macrocystis pyrifera*. The depth was 16 m and the substrate consisted of fine sands and silts with occasional stands of the brown alga, *Pterygophora california*, and patches of eelgrass, *Zostera marina*.

On 6 November 1979, five consecutive otter trawls of 10-min duration each were taken. The 3.7 m otter trawl was equipped with a cod end of 1.8 cm square mesh. Immediately following retrieval of the catch, sanddabs were sorted and placed in sealed plastic bags. Any *L. vulgaris* wandering about the catch were also retained. After the last trawl, four scuba divers entered the water and collected sanddabs by hand net, attracting fish with bait (sea urchin roe). Fish were transferred to sealed plastic bags. Specimens were collected in this manner for approximately 40 min. All fish and isopods collected by both methods were sexed and measured within the next day.

Host sex, total length to the nearest 0.1 cm, and number of parasitic isopods harbored were determined. Isopod total length was measured to the nearest 0.1 mm. Isopod sex was determined by several criteria: 1) Differential allometric relationship of width to length (Montalenti 1941), 2) presence of penes in males, 3) asymmetry of females, i.e., body twisted to the right or left (Brusca 1978), and 4) presence of oostegites in gravid females. Manca and aegathoid stages (see Brusca 1978) were lumped as juveniles.

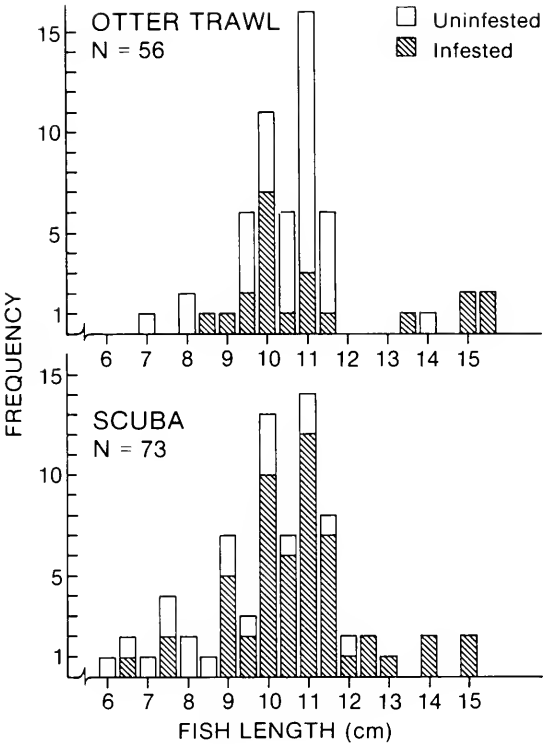

FIGURE 1.—Comparison of size-frequency histograms for *Citharichthys* spp. collected by otter trawl and divers utilizing scuba. Size distributions of sanddab hosts were similar (Kolmogorov-Smirnov test, $P>0.05$) but the percentage of hosts harboring parasitic isopods was significantly different (chi-square test, $P<0.005$).

Results and Discussion

Otter trawl catches consisted only of flatfish, and sanddabs comprised most of the catch. Size-frequency histograms for sanddab hosts collected by otter trawls and scuba divers were not significantly different (Fig. 1, Kolmogorov-Smirnov test, $P>0.05$). Inspection of these histograms indicates that divers are able to sample small fish more efficiently. Consequently, important information regarding the acquisition of isopod parasites by young fish may not be obtained when sampling with otter trawls. A comparison of the percent of fish infested with *L. vulgaris* reveals a highly significant disparity between the two sampling methods. In the trawl, 21 out of 56 hosts (37.5%) were infested versus 54 out of 73 hosts (73.9%) in the diver sample (chi-square = 17.449, $P<0.005$).

Size-frequency histograms for all isopods recovered by both collecting methods were significantly different (Fig. 2, Kolmogorov-Smirnov test, $P<0.05$). If only male isopods were considered, the difference was very significant ($P<0.01$) while for female isopods there was no difference ($P>0.05$). Apparently male *L. vulgaris* abandon hosts in otter trawls prior to retrieval of the catch. This was especially evident for small males (Fisher exact test, $P=0.0057$; small males <10.6 mm vs. large males ≥10.6 mm). Large males may also leave their hosts since a majority of large male isopods were unassociated with hosts in the trawl sample (13 out of 17 males, see Figure 2). In one trawl sample a pod of male isopods was found in the cod end indicating that these individuals did not have sufficient opportunity to escape. Female isopods have feeble crawling abilities (Brusca 1978) and do not appear to abandon hosts in trawls.

Relative parasite density in the diver sample was significantly higher (1.2 isopods per fish) than otter trawl samples (0.4 isopods per fish) (t-test, $P<0.001$) as was mean parasite intensity with 1.6 and 1.1 isopods per infested host, respectively (t-test, $P<0.001$).

In conclusion, otter trawls consistently underestimate prevalence, relative parasite density, and mean parasite intensity of *L. vulgaris* popu-

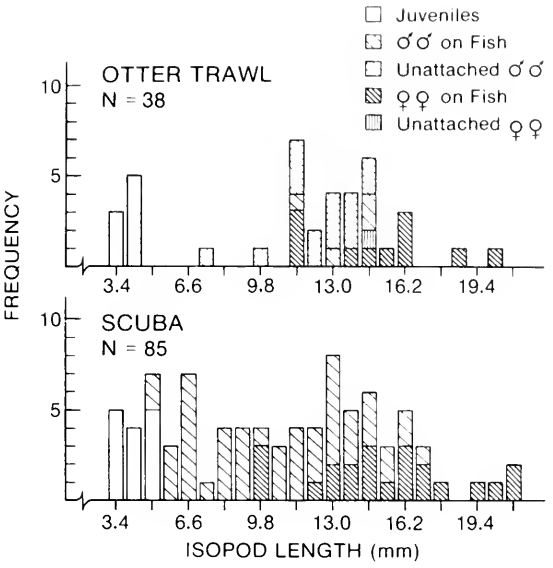

FIGURE 2.—Comparison of size-frequency histograms for the gill parasite, *Lironeca vulgaris*, from sanddab hosts collected by otter trawl and scuba divers. Size distributions of isopods were significantly different between the two samples (Kolmogorov-Smirnov test, $P<0.05$). Small male isopods were notably absent and several isopods were unattached to sanddab hosts in the otter trawl sample.

lations on *C. stigmaeus* and *C. sordidus*. This bias is caused by the abandonment of hosts, particularly by small male isopods. Shorter trawling times may reduce the amount of bias. However, when accuracy is desired, scuba is the preferred sampling method.

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443. Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. By Barbara Jayne Palko, Grant L. Beardsley, and William J. Richards. April 1982, iv + 28 p., 15 figs., 10 tables.
445. Sharks of the genus *Carcharhinus*. By J. A. F. Garrick. May 1982, vii + 194 p., 83 figs., 91 tables.

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753. Factors influencing ocean catches of salmon, *Oncorhynchus* spp., off Washington and Vancouver Island. By R. A. Low, Jr. and S. B. Mathews. January 1982, iv + 12 p., 6 figs., 7 tables.
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757. A profile of the fish and decapod crustacean community in a South Carolina estuarine system prior to flow alteration. By Elizabeth Lewis Wenner, Malcolm H. Shealy, Jr., and Paul A. Sandifer. March 1982, iii + 17 p., 8 figs., 5 tables.

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